On the Dynamics of Annual Plant Communities

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ABSTRACT

A reductionist approach to annual plant community dynamics is described. Community structure and change are interpreted in terms of the population dynamics of constituent species. This approach is put into practice in a series of experimental communities of annual crops and weeds.

Mathematical models of population dynamics are reviewed. Difference equation models of the dynamics of two competing populations are extended to three or more species; to species exhibiting seed dormancy; to populations controlled by an agricultural practice; and to the special situation in which a crop is sown at a constant density over generations.

This approach was applied to mixtures of three crop species, *Triticum aestivum* L., *Avena sativa* L. and *Sinapis alba* L., grown in pots over a wide range of densities and frequencies. Models fitted to seed changes in population size over one generation by non-linear regression predicted that mixtures will move towards a monoculture of *Sinapis* from any initial composition, equilibrium being reached by damped oscillations. An experiment to determine the effect of a selective herbicide on the dynamics of this system was also conducted.

Over a period of $2^1/_2$ years, the dynamics of a community consisting of four annual weed species, *Bromus sterilis* L., *Avena fatua* L., *Galium aparine* L. and *Sinapis arvensis* L., were monitored in field plots in the presence of a winter wheat crop. Replicate communities were subjected to a range of agricultural practices. Concurrently,binary mixtures of these weed species were grown in the field in the presence of the crop over a wide range of densities and frequencies. Models incorporating seed dormancy were fitted to changes in population size over one generation. These models predicted that whilst mixtures of *Bromus* and *Galium* would move towards stable coexistence, *Avena* populations would decline to extinction in the presence of *Bromus*. *Sinapis* declined towards extinction in the presence of winter wheat even in the absence of other weed species.

Observations from the $2^1/_2$ year study supported the predictions that *Bromus* and *Galium* should move towards stable coexistence and that *Sinapis* populations should decline. *Avena*, however, appeared to be maintained in the community without showing signs of reaching an equilibrium density. Possible explanations of this discrepancy between prediction and observation are given. Differences in management practice altered the nature of the community both qualitatively and quantitatively.

It is concluded that this approach has merit both in the interpretation of community structure and in the practical prediction of weed population sizes where more than one serious weed species is present. Further levels of experimentation required to generate practically useful predictive models are indicated. The complexity of communities to which this approach could be applied appears to be limited only by the size of necessary experiments.

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Chapter 1.

General Introduction.

'Predicting structural patterns of communities from the population dynamics of the constituent species clearly remains a vital unsolved problem.'

Gray *et al.* (1987).

Plant Populations and Communities.

A plant population consists of all individuals of a single plant species present in a given area. A plant community consists of all individuals of all plant species present in an area. These definitions beg the question "how is the area defined?" There is no general answer to this question. For the purposes of investigation, populations and communities are taken to occupy geographically defined areas or areas appearing uniform to the observer. Most often, however, one or more small, local samples are taken as typifying a population or community whose extent is rarely specified. These definitions force the conclusion that communities consist entirely of populations. Despite this, very different questions are asked of populations and communities. Areas of interest relating to populations include structure in terms of age or size of individuals, the rates and timing of birth and death, the relationship between density of individuals and population growth, and the regulation of population size. Studies of communities relate to such questions as species

composition (qualitative and quantitative), diversity, niche relationships, productivity, and changes in community structure through time. Changes in plant community structure may be on a small or large spatial or temporal scale. The term "succession" is difficult to define precisely (Miles, 1987) but in general terms it involves large changes in species composition and physical structure of communities, and acts on a relatively long time scale. On shorter time scales or when successional change is prevented, (for instance by periodic disturbance or heavy grazing), changes in species composition are less dramatic and changes in the relative abundance of species take on a greater significance. These smaller scale changes may be termed community dynamics.

A central theme in community ecology is the study of coexistence of species (cohabitation in the stricter usage of Harper *et al.* (1961), since ecological rather than genetic interactions are of interest). Coexistence or its absence, and the time scale on which coexistence is stabilized or displacement occurs, are the basis of both community dynamics and attempts to find "assembly rules" (Diamond, 1975; Lawton, 1987) governing community structure. The competitive exclusion principle (Gause, 1934) states that the species which is the best competitor in a mixture will ultimately exclude others, since for plants even a small advantage in seed yield can lead to dominance over a long period when microsites for establishment are limited. Despite the logic of the principle, it clearly does not apply in nature, since natural communities almost invariably consist of several potentially competing species. The competitive exclusion principle acts, then, as a useful null hypothesis: any hypothesis to explain coexistence must show how competitive exclusion is avoided.

A number of hypotheses to explain coexistence of species have been suggested. Many are not mutually exclusive. The first and most basic is the mathematical demonstration that equilibrium coexistence is possible in a

truly uniform environment under some conditions. This is based upon various mathematical models of population dynamics and interactions, with more or less plausible biological bases (Begon and Mortimer, 1981; see also Chapter 2). This constitutes a refutal of the competitive exclusion principle under certain conditions, by challenging the assumption implicit in the principle that competitive ability is independent of density and frequency. Other hypotheses seek to explain how competitive exclusion is avoided, without denying the potential for it to occur. A second explanatory hypothesis states that the habitat is not uniform, and that competitive exclusion may operate within each microhabitat, favouring different species in each whilst giving an impression of coexistence in the whole habitat. Early evidence for this came from bird communities (MacArthur and MacArthur, 1961; MacArthur, 1964) but it has also been applied to plant communities (Ricklefs, 1977; Grubb *et al.*, 1982). Thirdly, the niches (possibly fundamental niches and certainly realized niches (Hutchinson, 1957)) of coexisting species are sufficiently different that competitive exclusion does not occur. There are a number of theoretical studies of how different coexisting species need to be (eg May and MacArthur, 1972; Roughgarden, 1976), but as yet no generally applicable theory. Tilman (1982) has produced predictive models of species coexistence based on their efficiency of use of different levels of limiting nutrients, but as yet this approach has been tested rigorously only in mixtures of planktonic algae (Tilman, 1977, 1981). The fourth hypothesis is that predators (Paine,1966) or herbivores (Tansley and Adamson, 1925; Harper, 1977) may promote coexistence and increase diversity by selectively feeding on those species which would otherwise become dominant. This may be a result of either an intrinsic preference for one species or frequency dependent feeding in which the most abundant species is preferentially consumed.

In these first four cases it is assumed that the coexisting species reach equilibrium. Another class of hypotheses is based upon the presumption that whilst competition tends to move the community towards an equilibrium state without coexistence, other factors prevent equilibrium being reached. The first of these "non-equilibrium" hypotheses proposes community processes being dominated by essentially random establishment events: in a uniform habitat, where establishment sites appear unpredictably in space and time and where there is a large overlap in species' resource and habitat requirements, "interspecific competition for space [is] a lottery in which no one species can consistently win" (Sale, 1977). It has also been suggested, with support from mathematical models, that in a patchy environment, non-equilibrium coexistence may be possible where one species is inferior in competition within the patches, but superior in dispersal between patches (Levins and Culver, 1971; Horn and MacArthur, 1972; Slatkin, 1974). Related to this is the idea of a highly divided resource providing stochastic refuges for species which would otherwise be excluded quickly (Atkinson and Shorrocks, 1981). Another possible cause of non-equilibrium coexistence is chaotic behaviour in a mixture of species. A number of discrete and continuous models of interacting populations predict that under certain conditions, densities of each species may change chaotically over generations, without reaching equilibrium (eg May, 1976, 1985). This chaotic behaviour is deterministic, but the dynamics of the species mixture are unpredictable when even the slightest error is present in the observed initial composition. It is determined purely by the interaction of the individuals and populations, and does not depend upon environmental variation. Yet another factor capable of preventing populations reach equilibrium levels and so potentially allowing coexistence is disturbance. It has been suggested (Grime, 1973; Connell, 1979) that a maximum number of species will coexist at intermediate levels of disturbance, since dominance will be

prevented, but a relatively large number of species can tolerate the level of disturbance. Despite many theoretical studies, there are relatively few experimental studies of community responses to disturbance (Sousa, 1980). Finally, seasonal variation can prevent equilibrium and with it, competitive exclusion. "Good" years for one species may be "bad" for another, and *vice versa*: there is some evidence for this in tundra plant communities (Chapin and Shaver, 1985). Seed banks or long life of individuals could, however, buffer both populations against the effects of this variation.

These ideas of coexistence and competitive exclusion are central to community dynamics since coexistence or its absence, the decline to extinction or rise to dominance of species, and their timescales, are the very substance of community structure and change. As this emphasis on coexistence of populations indicates, the study of community dynamics clearly must involve investigation of events and processes at the level of the interacting species' populations as well as description of the net changes in communities. There has, however, been philosophical controversy between those favouring holistic and reductionist approaches to ecology. Much of this has been related to the so-called "organismic" (Clements, 1916, 1928) and "individualistic" (Gleason, 1917, 1926, 1927) views of the nature of, in particular, plant communities and the processes which shape them. The controversy is still alive: for example, Harper (1982) reacts against a supposed general view that "the whole is more than the sum of the parts" and that "the behaviour of deliberately simplified systems is irrelevant to understanding", by stressing a reductionist approach to ecology. If the aim of a reductionist approach is to completely account for every aspect of higher order behaviour in terms of lower order processes, then it is likely to fail. If, however, the aim is to obtain some idea of how lower order processes interact and generate higher order effects, even if no single natural system is entirely accounted for, there is more hope for the approach. The reductionist,

like the holistic approach should be judged on the contribution to understanding it makes in practice, rather than be subjected to philosophical prejudice. There is a compromise to be made, and there is no conflict between some aspects of Clements' notion of climax and the experimental approach of reductionists (Levins and Lewontin, 1980; Crawley, 1986).

Experimental mixtures of a few plant species have a particular significance in the study of plant ecology, forming a level of organization intermediate between populations and most communities. Whilst they have the characteristics of communities, they are simple enough to be analyzed by the methods of population ecology and are amenable to mathematical modelling, as are single populations. Mixtures of plant species are discussed next, in the context of plant population dynamics.

Plant Population Dynamics

Despite some significant work on plant populations early this century (Tansley, 1917; Sukatschew, 1928; Clements *et al.*, 1929), most developments have been anticipated by work on animal populations. This is perhaps because management of insect pests, in which numerical population size is of practical importance, stimulated development of theoretical and practical approaches to population dynamics (Varley *et al.*, 1975). Modelling of population changes in terms of changes in numbers over one generation by differential equations (for continuous population growth) or difference equations (for discrete growth) driven by density has been a central theme. The differences in approach to the population dynamics of animals and plants are probably the result of differences in growth form. Most animals (with notable exceptions such as bryozoans) have a relatively invariant growth form and show far less variation in sizes of reproductively mature individuals than do most plants. Plants, on the other hand, generally

have a modular growth form (White, 1979) and are enormously plastic (Harper, 1977). This results in number of individuals being a less useful descriptor of the state of a plant population than of an animal population. In agriculture, yield of a crop per unit area is of practical importance, and a common approach in plant ecology has been to relate this to plant density at some stage in the growth of the crop (eg Donald, 1951).

Mathematical modelling of plant density responses began in the 1950s with yield per plant / density relationships, using reciprocal equations (Kira *et al.*, 1953; Shinozaki and Kira, 1956). Later, modelling of density dependent mortality in plant populations began. From the start, this area was dominated by investigation of the "-3/2 power law" of self thinning (Yoda *et al.*, 1963; White and Harper, 1970; Gorham, 1979) relating mean plant weight to density. At the height of enthusiasm for this law, the relationship

$$w = 10^4 N^{-3/2}$$

(where w is mean plant weight and N is density) was claimed to describe both the course of self thinning through time and an upper limit to possible biomass / density combinations (Hutchings and Budd, 1981; White, 1981). This preoccupation with a particular "law" has detracted from other, more empirical, approaches to mortality. Moreover, doubt has now been cast on its generality, at least as a descriptor of the time course of self thinning, as a result of statistical analysis of many data sets (Weller, 1987).

Neither yield / density relationships nor models of mortality deal with the whole life cycle of plants. Demography is the quantitative description of the life cycle. Apart from the study of population depletion curves (eg Tamm, 1972) which, whilst giving interesting information on the life span of individuals, do not deal directly with population size, many of the earliest studies of plant demography involved annual species. These include estimation of the rate of increase of a population of *Avena fatua* L. censussed annually for ten years (Selman, 1970), a detailed quantification of the life

cycle of *Alopecurus myosuroides* Huds. over a single year (Naylor, 1972), and the construction of life tables for populations of *Sedum smallii* (Britton) Ahles and *Minuartia uniflora* (Walt.) Mattf. (Sharitz and McCormick, 1972). Some of the first mathematical models of plant populations concentrated on description of structure in terms of age (following Leslie, 1945), growth stage (following Lefkovitch, 1965) or both (Law, 1983) and used matrices to describe probabilities of transitions between states. Early examples of the application to data from natural populations of difference equations in the form of matrix models include a study of three species of *Ranunculus* L. (Sarukhan and Gadgil, 1974) and a comparison of age and stage classification in populations of *Dipsacus sylvestris* Huds. (Werner and Caswell, 1977). Such matrix models are very different from those in which predictions of population change are driven by density. They extrapolate from the events observed over a time at field densities: they indicate the direction in which a population is changing at the time of study, but cannot predict the outcome of change. Introduction of transition matrix elements which are functions of density provides one way of overcoming this problem (Law, 1975; Mortimer *et al.*, 1978).

Preoccupation with the differences between animals and plants (eg Bradshaw, 1972) can obscure the similarities (Begon and Mortimer, 1981). Whilst plants are generally more plastic than animals, they retain individuality at the genetic and modular levels. In annual species, genetic individuals ("genets"; Kays and Harper, 1974) generally remain distinct, and it is possible to examine their population dynamics as for animal populations using simple algebraic difference or differential equations. This approach has only recently been taken, initially in populations of annual weeds. Populations of *Agrostemma githago* L. (Watkinson, 1981), *Bromus sterilis* L. (Firbank *et al.*, 1984, 1985) and *Avena fatua* L. (Manlove, 1985) have been modelled in this way. This type of modelling requires data from an

experiment in which the species is grown at a range of densities in pots or field plots and in which seed production is measured for each treatment. It also relies on the use of non-linear regression techniques to parameterize the models. Such simple difference equation models can be used to predict population dynamics, and are easily extended to mixtures of two or more species (Hassell and Comins, 1976). Moreover, some are analytically tractable (Chapter 2).

Experimental error is generally large enough that quite a large number of treatments are required in order to obtain a satisfactory fit when these models are used. The use of fan designs (Bleasdale, 1967) might appear to be one way of reducing the size of such experiments. In a fan design, plants are positioned in a series of concentric arcs forming a fan shape. Moving outwards, the distance between arcs and the distance between plants in each arc increases. Hence, the ecological neighbourhood area (Antonovics and Levin, 1980) of individuals increases progressively outwards. On the assumption that neighbourhood area is an index of the individual's perception of density, each row is taken as being at a different density. However, neighbourhood area is not a true index of "density about an individual" since size of neighbours in a size-distributed population as well as distance from neighbours influences individual performance. The greatest difficulty with fan designs is that a plant's neighbours do not have the same neighbourhood areas as the plant itself, and that this variation is systematic, plants on one side having a greater, on the opposite side having a smaller, and on the remaining two sides having the same size neighbourhood area. The situation is not the same as that in a plot with uniform plant density. Fan designs are also prone to generate edge effects which are propagated in a wave-like fashion throughout the design. Plants in the outside row have no neighbours on one side: these plants are then unexpectedly large, resulting

in those in the next row being unusually small, repeating in a damped convergent manner (Chang, 1982).

Considerations of individuals' neighbourhoods, such as these, has led to a spate of "neighbourhood models" of population dynamics. These are based on the construction of mathematical relationships between the number of other individuals within some neighbourhood area (whose radius is defined either arbitrarily, or empirically as resulting in the best fit) and survivorship or fecundity. These relationships have various forms (Mack and Harper, 1977; Weiner, 1982; Watkinson *et al.*, 1983; Pacala and Silander, 1985). Neighbourhood-based models of seed dispersal have also been constructed (Pacala and Silander, 1985). Predictions of population dynamics are made by applying the survivorship, fecundity and dispersal models to every individual in a population. A vast amount of data is required in order to fit this type of model, since, like matrix models, they attempt to classify the members of the population, though the classification is by proximity to neighbours rather than by age or growth stage. Schaffer and Leigh (1976) contend that the mathematics of neighbourhood models is intractable and suggest that because of this a theory of population dynamics adequate for plants may be unachievable. Even if the analytically tractable models of Pacala and Silander (1985) prove to be unworkable, this is not necessarily true. Whilst classification of population structure can be particularly rewarding in plants, since they are generally more plastic and less mobile than most animals, simple numerical consideration of population size is as valid for plants as for animals.

Fan designs and neighbourhood approaches do not, then, provide suitable alternatives to experiments in which the seed production of a species is measured when it is grown at a range of densities. The approximation to a given density achieved in one arc of a fan design is poor and subject to systematic error. Neighbourhood models, even if they prove to be viable,

require even larger experiments than do density based models of population performance, and for the purpose of predicting population dynamics include an unnecessarily large amount of information at the level of the individual. When predictive models of plant population dynamics are required, difference equations fitted to yield data from a range of densities appear to provide the best compromise between rigour and practicality.

Dynamics of Mixtures.

For many years, animal ecologists have utilized various experimental and modelling techniques for studying the dynamics of mixtures of species as well as of single populations. These include differential and difference equation models of two species interacting through competition, predation or parasitism (Varley *et al.*, 1975). Research on interspecific competition in plants has a long history, but only recently have results been related directly to population dynamics. More emphasis has been placed on the study of competition in its own right, on the comparison of mixture *versus* monoculture yields, which has practical value in evaluating the yields of mixed cropping systems, and, related to this, on identifying niche separation. Until the last few years, most experimental designs have fallen into three categories, additive designs, replacement series and mechanical diallels. In an additive design (eg Welbank, 1963) the density of one species is held constant whilst that of the other is varied. In a replacement series (de Wit, 1960), total density is held constant whilst the relative frequencies of the two species are varied. de Wit developed techniques for analyzing the results of replacement series based on a mathematical analogy with Raoult's law of the partial vapour pressures above a binary mixture of liquids. A measure of aggressiveness of one species towards the other, the relative crowding coefficient, can be calculated as the ratio of the per plant yield ratio in mixture

to the per plant yield ratio in monoculture (de Wit, 1960). The concept of relative yield total (RYT), defined as the sum of the ratios of yield in mixture to yield in monoculture for each species (de Wit and van den Bergh, 1965), is a commonly used comparison of mixture versus monoculture yields. It has been promoted as an indicator of niche or limiting resource relationships, notably by Harper (1977): RYT values of 1 are claimed to imply a common limiting resource whilst RYT>1 suggests different limiting resources or niche separation. The third type of design, the mechanical diallel, is rather different in that it is used to investigate competitive relationships within a larger group of species. Each species is grown in pure stand and in all possible binary mixtures at a relative frequency of 1:1. Analysis of variance is used on various treatments of yield data (McGilchrist, 1965; McGilchrist and Trenbath, 1971) in order to determine the magnitude of competitive effects. The results of those studies using the technique (eg Norrington-Davies, 1967) are hard to understand, and the results are not easily related to population dynamics. Trenbath (1978) has attempted to predict equilibrium states of mixtures from the results of diallels. This approach assumes that competitive effects are similar across a range of densities and frequencies, an unlikely occurrence, and so is of little value.

Additive designs have been criticized because the effects of density and frequency are confounded (Harper, 1977). In the few real situations in which one species is only found at one density whilst the other can vary (eg a crop and a weed) this approach may, however, be relevant (eg Butcher, 1984). Replacement series have also been widely criticized (Connolly and Nolan, 1976; Jolliffe *et al.*, 1984; Firbank and Watkinson, 1985; Connolly, 1986). Some of these criticisms relate to measures of competitiveness and mixture versus monoculture comparisons which are not directly relevant to the modelling of mixture dynamics. For example, Connolly (1986) shows that RYT can only be used to measure the efficiency of resource use by a mixture

if pure stand yields are independent of density, a crippling assumption. A better index, relative resource total (RRT), which represents the total pure stand area required to produce the same yield as a unit area of a given mixture, is described by Connolly (1987). The use of RRT is not restricted to the results of replacement series. If yield data from mixture experiments are being used to predict mixture dynamics, the most serious criticism of both additive and replacement series designs is that they do not allow exploration of a wide range of densities and frequencies. The results are applicable only to the density used in the experiment, and no generalizations about the yields of other mixtures can be made. Such constraints prevent prediction of mixture and community dynamics.

More satisfactory designs are those which are based on varying density and frequency independently, allowing investigation of a more thorough range of mixtures. This is often achieved by taking a range of densities of each species and growing them together in all possible pairwise combinations (the addition series, eg Firbank and Watkinson, 1985). This type of design overcomes most of the problems inherent in replacement series and simple additive designs, the cost of this being a larger experiment. These designs are particularly suitable when competition is to be related to the dynamics of a mixture. They may be analyzed using difference equation models similar to those used for competing animal species (Firbank and Watkinson, 1985; Law and Watkinson, 1987) and allow prediction of mixture dynamics.

Annual Plant Communities.

Annual plant communities provide interesting examples for study. They may be defined as communities which show inherent stability in species composition whilst suffering periodic (often seasonal) disturbance which

precludes the survival of plants in an active photosynthetic state. Characteristically, species exhibit traits which enable them to survive such perturbations: clonal species possess rhizome / stolon bud banks whilst non-clonal ("unitary") ones survive as a result of alternation between seed and plant state. Sand dune annual plant communities, often characterized by very low species diversity, show considerable stability (eg Symonides, 1984) in the face of regular seasonal disturbance. Experimental studies (eg Watkinson, 1984) illustrate that the stability of population sizes occurs through the interaction of density dependent and density independent factors. In these communities, intraspecific regulation would appear to dominate the set of biotic interactions, predators, whilst occuring, being of much less importance. Contrasting annual plant communities are those which suffer periodic disturbance and intense interspecific, as well as intraspecific, competition, as exemplified by arable communities. Such communities are arrested in development by the imposition of agricultural practices (eg cultivation, herbicides). They provide the setting for the research described in this thesis.

The Approach Taken in this Thesis.

As discussed earlier, a number of factors may influence community dynamics. These include competition, predation, disease, disturbance (both its magnitude and its frequency), habitat size and heterogeneity within the habitat (both in space and time). Of these, the effects of competition are always density dependent, whilst those of the others may or may not be. For this reason, competition is of particular interest, since its effects are determined by the very factor they affect, the densities of each species in the community. This gives it a strong appeal as the basis for mathematical modelling approaches.

Whilst the role of competition in determining or maintaining community structure has been demonstrated in some plant communities by selective removal experiments (eg Putwain and Harper, 1970), it is especially evident in the annual plant communities of arable cropping systems. The entire history and literature of weed control testify to this. It could be contended that the annual disturbance associated with the cropping cycle is a more important determinant of community dynamics: without it, perennial herbaceous and woody species would undoubtedly become established, as the many studies of old field succession show (eg Keever, 1950). However, it may be more useful to consider this disturbance to be a constant feature of the environment in which competitive interactions take place. After all, as Crawley (1986) points out, competitive ability (and hence the outcome of competition) is not a species attribute, but depends upon both the environmental conditions and the other plant species involved. Annual disturbance can be seen as preventing large scale successional change, whilst competition drives smaller scale community dynamics within the *milieu* of an arrested successional stage. Variations in other factors are seen as modifying these basic competitive processes.

In this approach, then, competition is seen as driving community dynamics. Other, invariant, factors make up the background against which competitive interactions take place. Yet more factors which may vary, whether man-imposed husbandry practices or natural events, are seen as modifiers of competitive effects. Four experimental chapters of this thesis describe investigations of annual plant community dynamics, following this rationale, in increasingly complex and realistic situations. Chapter 3 describes a study of the dynamics of a mixture of 3 annual crop species without seed dormancy growing in pots using an experimental design in which density and frequency are varied independently. In Chapter 4, the same system is investigated with and without the application of a modifying factor, a selective

herbicide. Chapter 5 describes competition experiments in binary mixtures of annual weed species, some exhibiting seed dormancy and protracted germination periods, in the presence of a crop in field plots. In Chapter 6, a study of the dynamics over $2^1/_2$ years of weed communities consisting of those species investigated in Chapter 5 is described: community dynamics are studied under a range of husbandry regimes, in order to discover the effects of these modifying factors on the nature of and progress to equilibrium community structure. First, however, the mathematical models used in these studies will be discussed in Chapter 2.

Chapter 2.

A Mathematical Approach to Annual Plant Community Dynamics.

'Human kind cannot bear very much reality.'

T.S.Eliot.

Density Dependence.

As discussed in Chapter 1, the approach to community dynamics taken in this thesis is based upon the densities of the plant species which make up the community. Density dependent processes are seen as driving the dynamics of the community, whilst environmental factors and agricultural practices are seen as modifiers of these processes. This distinction between 'intrinsic' density dependent processes and 'extrinsic' modifying factors is artificial. A population of plants exists in its environment, and interactions between individuals are mediated by that environment. For example, competition between individuals for resources operates through resource depletion in the environment, whether the resource is a growth requirement or space in which other resources are distributed. However, simplification is the essence of modelling, and the distinction is convenient. Whether 'intrinsic' or 'extrinsic' processes are taken as the basis for an approach will depend on the object of study. In an investigation of the origin of differences

in community composition between different parts of a sand dune system, one might take environmental differences as a basis. If, however, one is interested in the long-term dynamics of a serious weed in a crop, or the population dynamics of an abundant sand dune annual, then the approach starting from density dependence may be relevant.

Modelling can be carried out at two levels, by following generation to generation changes in population size based upon mean performance, or by following a group of individuals within and over generations. Population changes may be modelled simply as the number of individuals, or in more complex ways (for example Markov chain models of the dynamics of populations which are age-distributed (Leslie, 1945), growth stage-distributed (Lefkovitch, 1965) or both (Law, 1983)). The simplest approach has been taken in this chapter, developing models of simple population size changes between generations, based upon mean performance of individuals.

A population of annual plants with discrete generations and no persistent seed bank will be considered first. Density dependent population processes may be modelled by equations of the form

$$Y = N\,g(N) \qquad (1)$$

where N is density, g(N) is some function of N, the growth function, and Y is some indication of population, rather than individual, performance measured on a unit area basis. The process whose effect is modelled will vary according to the nature of Y and the point in the life cycle at which N is assessed. For example, if N is density immediately after germination, and Y is density of mature plants, the model will relate to density dependent mortality. Similarly, if N is seed production per unit area in one generation, and Y is seed production in the next, then the model will relate to population changes over a complete generation. Most models used in this study are of this second type.

Some authors, following Kira *et al.* (1953) model individual, rather than population performance. In this case,

$$Y_i = f(N) \qquad (2)$$

where Y_i is some indicator of mean individual performance and f(N) is some other function of N.

The growth function, g(N), may have many forms. Bellows (1981) compared seven growth functions theoretically and favoured two in terms of their generality of form:

$$g(N) = \exp(-a N^b) \qquad (3)$$

$$g(N) = (1 + (a N)^b)^{-1} \qquad (4)$$

where a and b are experimentally determined parameters. Of these, equation (4), due to Maynard Smith and Slatkin (1973), was found to provide better fits to a range of insect survivorship data. Law and Watkinson (1987) fitted models of interspecific competition based on eight different monoculture growth functions to yield data from mixtures of two sand dune annuals. Models derived from two growth functions were found to give the best fits. These growth functions were

$$g(N) = \lambda (1+aN)^{-b} \qquad (5)$$

due to Hassell (1975), and

$$g(N) = \lambda (1+N^b)^{-1} \qquad (6)$$

In both cases, λ is the maximum attainable yield of one individual under uncrowded conditions. Equation (6) was ultimately preferred, having a more general form, although this was in a 2-species derivative. There is a similarity of form between these functions and equation (4).

Dynamics of Monocultures.

Changes in population size over one generation can be modelled as

$$N_{t+1} = N_t\, g(N_t) \qquad (7)$$

where N_t is population size at some stage of the life cycle in one generation, and N_{t+1} is the population size at the same stage in the next generation. Hence, taking the growth functions of equations (5) and (6) we have

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b} \quad (8)$$

and

$$N_{t+1} = \frac{\lambda N_t}{1 + N_t^b} \quad (9)$$

Equation (8) will be referred to colloquially in this thesis as the "Hassell model". In both these cases, λ is now more specifically the asymptotic per capita rate of increase at low densities. This type of model can be iterated to predict population size after a given number of generations.

These models apply to monocarpic plants with discrete generations. Furthermore, they assume simultaneous germination, although if an extended germination period has the same frequency / time distribution each year, the models are still adequate. If any of these assumptions are relaxed, then Markov chain models using vectors to describe population structure and matrices to describe probabilities of transition between states of individuals may be more appropriate.

Dynamics of Mixtures.

The usual starting point for models of species mixtures is the Lotka-Volterra model (following Lotka, 1925; Volterra, 1926), a two species extension of the logistic equation. However, this is a differential equation modelling continuous population growth. Where generations are discrete, models may be based instead on the difference equation models discussed above. Consider the effect of introducing individuals of a second species into a monoculture. The effect will normally be to reduce the yield (per area and per capita) of the first species. However, the addition of the same number of individuals of the first species would also lead to a per capita yield reduction,

though probably not of the same size. This suggests that (following Hassell and Comins, 1976) the effect of a second species on the yield of the first could be modelled by modifying the growth function so that an individual of the second species is equivalent to a certain number (or fraction) of individuals of the first species in its effect on the yield of the first species, i.e.

$$g'(N_1) = g(N_1 + \alpha N_2) \qquad (10)$$

where g'(N1) is the modified growth function for species 1 and α is a constant, the equivalence coefficient. This assumes that α is constant over all densities and relative frequencies of the two species. Similarly for species 2,

$$g'(N_2) = g(N_2 + \alpha_2 N_1) \qquad (11)$$

where α_2 is another equivalence coefficient. In this way, the Hassell model can be extended to a pair of equations (following Hassell and Comins, 1976):

$$N_{1t+1} = \frac{\lambda_1 N_{1t}}{(1 + a_1(N_{1t} + \alpha_1 N_{2t}))^{b1}}$$

$$N_{2t+1} = \frac{\lambda_2 N_{2t}}{(1 + a_2(N_{2t} + \alpha_2 N_{1t}))^{b2}} \qquad (12)$$

The 2 species model favoured by Law and Watkinson (1987) is an extension of equation (9) in a rather different way:

$$N_{1t+1} = \frac{\lambda_1 N_{1t}}{1 + N_{1t}^{b1} + N_{2t}^{b2}}$$

$$N_{2t+1} = \frac{\lambda_2 N_{2t}}{1 + N_{2t}^{b'1} + N_{1t}^{b'2}} \qquad (13)$$

This model is referred to colloquially in this thesis as the "Law and Watkinson model". It does not have explicit equivalence coefficients, and so the assumption of constancy over density and frequency is relaxed. However, mathematical generality is achieved at the cost of biological significance and the potential for its properties to be investigated analytically rather than by simulation.

The way in which these models may be extended to n species is illustrated by the 3 species case. For the Hassell model:

$$N_{1t+1} = \frac{\lambda\, N_{1t}}{(1 + a(N_{1t} + \alpha N_{2t} + \beta N_{3t}))^b} \qquad (14)$$

plus two other equivalent equations for species 2 and 3. α and β are assumed to be constant over all combinations of densities of all three species. For the Law and Watkinson model:

$$N_{1t+1} = \frac{\lambda\, N_{1t}}{1 + N_{1t}^{b1} + N_{2t}^{b2} + N_{3t}^{b3}} \qquad (15)$$

plus two other equivalent equations. Iteration of any of these mixture models can be used to predict changes in composition of mixtures over a number of generations.

Persistent Seed Banks.

A population of annuals with discrete above-ground generations, as before, but in which seed can survive in the soil for at least one generation will now be considered. The Hassell model (equation 8) can be extended in this way:

$$N_{t+1} = \frac{\lambda'\, N_t}{(\,1 + a' N_t\,)^b} + SN_t \qquad (16)$$

where S ($0 \le S \le 1$) is the density-independent fraction of N_t surviving in the seed bank to the next generation. SN_t is separated from the rest of the equation because density dependent growth processes do not act on this fraction of N_t. λ' and a' are not equal to λ and a in equation (8) (except where S=0) because the fraction of N_t on which density dependent growth processes act is smaller.

This formulation may be analyzed in more detail. Seeds making up the initial population have three possible fates: death, germination, or remaining

dormant. If the proportion of seeds suffering each of these fates is density independent, then

$$S + D + G = 1$$

where D and G are death and germination rates constant over generations. The proportion of N_t on which density dependent growth processes act is GN_t , i.e. N_t (1-S-D). These models can be related to more fundamental growth models which relate fecundity to the density of just those seeds which germinate, by writing

$$\lambda' = \lambda_f (1 - S - D)$$

$$a' = a_f (1 - S - D)$$

where λ_f and a_f are the constants in the fundamental density dependence functions. In the simpler case of the usual Hassell model (equation 8), S=0, so that

$$\lambda = \lambda_f (1 - D)$$

$$a = a_f (1 - D)$$

This treatment of components of N_t demonstrates that the form of the growth function is still applicable when a persistent seed bank is present, even when the model is fitted to N_t rather than GN_t. λ and a are simply scaled accordingly. However, if seed bank death or germination rates are density dependent, modelling is more difficult. At best,

$$N_{t+1} = \frac{\lambda'' N_t}{(1 + a'' N_t)^b} + N_t f(N_t) \qquad (17)$$

where f (N_t) is some function of N_t and where λ" and a" reflect changes in λ_f and a_f. At worst, density dependent seed bank processes might not be modellable by this form of relationship. (This relationship could already be thought of as a combination of a mortality relationship and a fecundity relationship as Watkinson (1980) considers.) Some different, probably more complicated, model would then be required (MacDonald and Watkinson, 1981).

It is important that whilst equation (8) can legitimately be fitted to seed bank - seed bank, seed at harvest - seed at harvest, or plant - plant data, equation (16) may only be fitted to seed bank - seed bank data.

Seed dormancy can be incorporated into models of mixtures with no additional assumptions. For example, each equation of the two species Hassell model (equation 12) will take on the form:

$$N_{1t+1} = \frac{\lambda' N_{1t}}{(1 + a'(N_{1t} + \alpha N_{2t}))^b} + S N_{1t} \qquad (18)$$

Weed and Crop Situations.

a) Modelling Weed Yield in Uniform Density of Crop.

Arable crops are generally annual species sown at the same density each year. These models can be of use in predicting the population dynamics of weeds in arable fields repeatedly sown with the crop, as is often the case with winter wheat in the U.K.. Practically, the unmodified Hassell model (equation 8) or its form incorporating a seed bank (equation 16) can be fitted to weed yield data when a crop is sown at constant density N_c. The crop is then considered to be part of the environment, albeit one which can alter the regulatory processes of the weed population. The model is formally incorrect in this situation, but identical in construction to the correct model. The normal two species model for the weed in the presence of the crop would be (from equation 12):

$$N_{t+1} = \frac{\lambda N_t}{(1 + a(N_t + \alpha N_c))^b}$$

where N_c is crop density. When N_c is constant, however, this simplifies to:

$$N_{t+1} = \frac{K_1 N_t}{(1 + K_2 N_t)^b} \qquad (19)$$

where $K_1 = \lambda (1 + a\alpha N_c)^{-b}$, a constant,

and $K_2 = a (1 + a\alpha N_c)^{-1}$, also a constant.

This, then, has the same form as the single species Hassell model. The definitions of the parameters K_1 and K_2 imply a high degree of interdependence between the values of K_1, K_2 and b.

In the same way, the two species Hassell model (equation 12) can be extended for two weed species in a crop. Each of the pair of equations will have the form

$$N_{1t+1} = \frac{K_3 N_{1t}}{(1 + K_4 (N_{1t} + \alpha N_{2t}))^b} \qquad (20)$$

where $K_3 = \lambda (1 + a\beta N_c)^{-b}$, a constant,

and $K_4 = a (1 + a\beta N_c)^{-1}$, also a constant.

The form is that of the normal two species Hassell model. Again, extension of the seed bank case (equation 16) leads to

$$N_{t+1} = \frac{K_5 N_t}{(1 + K_6 N_t)^b} + S N_t \qquad (21)$$

where $K_5 = \lambda' (1 + a'\alpha N_c)^{-b}$, a constant,

and $K_6 = a' (1 + a'\alpha N_c)^{-1}$, also a constant.

The conclusion is that it is legitimate to fit the Hassell models to populations of weeds in the presence of a constant density of a crop without incorporating an N_c term into the models.

b) Modelling Crop Yield in the Presence of Weeds.

It can be useful to model the yield of a crop sown at a constant density in the presence of a weed species at any density. Keeping within the framework of the Hassell model, the normal two species case would be

$$N_{ct+1} = \frac{\lambda N_{ct}}{(1 + a_c(N_{ct} + \alpha N_t))^{bc}} \qquad (22)$$

crop parameters being subscripted "c". When N_{ct} is constant over generations, this simplifies to

$$N_{ct+1} = \frac{C_1}{(1 + C_2 N_t)^{bc}} \qquad (23)$$

where $C_1 = \lambda N_{ct} (1 + a_c N_{ct})^{-bc}$, a constant,

and $C_2 = a_c \alpha (1 + a_c N_{ct})^{-1}$, also a constant.

C_1 describes the weed free yield of the crop sown at density N_{ct}.

Proportional yield loss, Y_l is defined by

$$Y_l = 1 - \frac{\text{crop yield in presence of weed}}{\text{weed free yield}} \qquad (24)$$

Hence, $$Y_l = 1 - (1 + C_2 N_t)^{-bc}$$

giving $$Y_l = \left(\frac{C_2 N_t}{(1 + C_2 N_t)} \right)^{bc} \qquad (25)$$

Specifically, where b_c=1, the yield loss is

$$\frac{C_2 N_t}{(1 + C_2 N_t)}$$

With this constraint and in the case where yield loss approaches 100% at infinite weed density, this yield loss model is identical to that proposed by Cousens (1985). Equation (25) provides a general description of proportional yield loss whether or not the law of constant final yield loss (b=1) pertains. This formulation hinges on the assumption implicit in equation (12) that crop and weed species may be equivalently expressed in terms of each others densities. The parameter b_c reflects the crop's response to its own high density. This interchangeability rests on the equivalence assumption.

Mixtures of two or more weed species in the presence of a crop sown at constant density over generations can be treated in a similar way. Further, these crop yield models do not lose applicability in the presence of persistent weed seed banks. Assuming that S, D and G are density independent, N_t can be taken as density of weed seeds in the seed bank or density of germinating plants. However, if the state variable N_t is taken to be the density of weeds at harvest (N_h), the model loses relevance. Competitive effects determined by the density of weeds earlier in the season themselves determine both crop yield and harvest density of weeds. Should N_h be used as the state variable, the density dependence model of equation (23) would

be fitted to a relationship based on two interacting density dependent processes, one determining yield in the crop, the other determining survivorship in the weed. This is a problem inherent in any attempt to predict crop yield from harvest density of weeds, not of this modelling approach in particular.

Control Practices.

In the approach to population and community dynamics taken in this thesis, environmental variation and agricultural control practices are argued to be modifiers of "intrinsic" density dependent processes. The way in which these practices are modelled must depend on the nature of their effects. Some types of density dependent effects of control could be incorporated into the basic Hassell model, simply by altering parameter values. Still within the framework of the Hassell model, equation (8) can be extended to include the effect of a density independent control practice:

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b} - \Lambda N_t \qquad (26)$$

where control is exerted as a proportion, ρ, of λ (i.e. where $\Lambda = \rho \lambda$) (P. Gould and A. M. Mortimer, pers. comm.).

Extended into two species, only one of which experiences a density independent control practice, equation (12) becomes:

$$N_{1t+1} = \frac{\lambda_1 N_{1t}}{(1 + a_1(N_{1t} + \alpha_1 N_{2t}))^{b1}} - \Lambda N_{1t}$$

$$N_{2t+1} = \frac{\lambda_2 N_{2t}}{(1 + a_2(N_{2t} + \alpha_2 N_{1t}))^{b2}} \qquad (27)$$

For some types of density dependent effects of control practices, models of a quite different form may prove necessary. For example, in a situation in which the effect of a herbicide was greater at lower densities, the "predator

pit" model of Holling (1965) has been used successfully (P. F. Ulf-Hansen and A. M. Mortimer, pers. comm.). This model has the form

$$N_{t+1} = \frac{\rho N_t^2}{(K + N_t^2)} \qquad (28)$$

where ρ and K are constants.

Analytical Treatment of Models.

The equilibria and their stability predicted by these monoculture and mixture models can be explored by computer simulation. However, some models are also analytically tractable. This provides a more rigorous and mathematically more elegant way of finding equilibria and analyzing their stability.

For the monoculture Hassell model it can be shown that the equilibrium density is

$$\frac{\lambda^{1/b} - 1}{a} \qquad (29)$$

Stability conditions are :

monotonic stability	$0 < b(1 - \lambda^{-1/b}) < 1$
stability (convergent oscillations)	$1 < b(1 - \lambda^{-1/b}) < 2$
instability (divergent oscillations)	$2 < b(1 - \lambda^{-1/b})$

Analytical treatment of the two species Hassell model and density independent control models are also available (Hassell and Comins, 1976; P. Gould and A. M. Mortimer, pers. comm.)

To summarize, this chapter describes and develops an approach to annual plant community dynamics based upon difference equation models of population change over generations. Extensions to multiple species situations, populations with persistent seed banks, and populations subject

to control practices have been discussed. The special case of weeds in the presence of crops has been considered, and a yield loss model derived from a population dynamics model has been shown to be homologous under certain circumstances to a previously published model formulated especially for yield loss. The application of these theoretical models to real situations depends upon the use of non-linear regression techniques to fit models to experimental data. The following chapters make the link between theoretical models and real populations and communities, in a series of increasingly complex systems.

Chapter 3.

Competition in Mixtures of Three Annual Crop Species.

"It may be taken as axiomatic that the influence of one species upon another in a struggle for existence increases as the density of the species increases. It is therefore extremely important to relate observations on a struggle for existence to the changing densities under which the struggle may occur.

Harper *et al.* (1961).

Introduction.

One reason for studying the effects of plant competition is to predict the yields of crops, whether grown on their own at various densities, in mixtures, or in the presence of weeds. Most studies of competition between plant species have involved crops and / or weeds (Harper, 1977, and references therein). They usually involve sowing mixtures of the species at a range of densities and/or relative frequencies and measuring the resulting yield of both species. Until recently, most such experimental designs have fallen into one of two categories, additive designs (eg Welbank, 1963), in which density of one species is varied whilst that of the other is held constant, or replacement series (de Wit, 1960), in which total plant density is held

constant whilst the relative frequencies of the species are varied. As discussed in Chapter 1, both these designs are of limited interest because their conclusions are restricted to a single density of one or both species. Other designs in which both species are sown at a range of total densities and relative frequencies overcome this problem. Published studies using such designs (Firbank and Watkinson,1985; Law and Watkinson,1987) are restricted to two species. Extensions of this approach to mixtures of 3 species, and on to the general n-species case, greatly increase the size of experiments and add to the complexity of mathematical models required to interpret the results. However, this extension brings the approach to a level where it could be used to study competition in communities.

There is a second reason for studying plant competition. Iteration of a model of the effects of competition on seed production over one generation allows the prediction of the composition of the mixture after a given number of generations. This enables one to investigate the dynamics of interacting populations. When this is the reason for study, replacement series and additive designs are of no use, because densities and frequencies are likely to move beyond the bounds of one of these designs in a single generation. Only designs in which both density and frequency are widely varied can provide sufficient information.

This experiment uses a three-species design of this type. The results are used to generate predictive models of seed yield of each species in terms of sowing densities of all three species. These models are then iterated to investigate the dynamical properties of the mixture. This experiment represents the simplest and perhaps the least realistic of the systems to which this approach to annual plant community dynamics is applied in this thesis. Its novelty lies in the independent variation of densities of three species.

Materials and Methods.

The crops used in this experiment were spring wheat, *Triticum aestivum* L. cv Bounty, spring oats, *Avena sativa* L. cv Dula, and a commercial stock of white mustard, *Sinapis alba L.*. Crop species were chosen in order to create a simple system. They exhibit little seed dormancy and germination is more or less synchronous. Moreover, these strains are highly inbred, minimizing the amount of genetic variation within the population. These particular species were chosen so that one (*Sinapis*) was different in many ways from the other two. It is a dicotyledonous crop rather than a cereal, and exhibits aerial branching rather than basal tillering. It is an indeterminate species, flowering and setting seed over a long, probably environmentally determined period as opposed to the determinate cereals whose tillers flower and set seed almost synchronously. The experiment was carried out in an unheated polythene tunnel at the University of Liverpool Botanic Gardens, Ness, Cheshire. Plants were grown in pots of area $0.056m^2$ in John Innes No.1 compost. Wheat and oats were sown at a depth of 50 mm, mustard at a depth of 5 mm.

The design included monocultures of each species, mixtures of each of the three possible pairs of species, and mixtures of all three species. Monocultures were sown at densities of 1, 6, 18, 54, 162, 486, 1200, 3000 and 8000 seeds per pot (18 to 140000 seeds m^{-2}). In addition, monoculture densities of 1 plant in larger pots of area $0.18m^2$ were sown. The ratio of soil volume to soil surface area was held constant. Binary mixtures were sown at total densities of 2, 6, 18, 54, 162 and 486 seeds per pot (36 to 8700 seeds m^{-2}) and at frequencies of 1:1, 2:1 and 1:2 at each density except the lowest. Ternary mixtures were sown at total densities of 6, 16, 54, 162 and 486 seeds per pot (110 to 8700 seeds m^{-2}) at frequencies of 1:1:1, 4:1:1, 1:4:1 and 1:1:4 at each density. There were three replicates. Each set of replicates was laid out as a block, pots being assigned randomly within the

blocks. In addition, a fourth replicate of each monoculture treatment was randomly assigned to one of the blocks.

All pots were sown on 16th May 1986. Pots were watered daily, and in the later stages of the experiment the fungicides bupirimate and triforine were applied prophylactically at fortnightly intervals, each at a concentration of 41mg l^{-1}. Strings were tied to canes around each pot to prevent lodging.

Seedlings were counted soon after germination. In any pot in which 12 or fewer seeds of a species were sown, transplants were made from spare pots to compensate for seeds failing to germinate. Surplus plants in pots were removed. The layout of pots was re-randomized once during the growing season in an attempt to reduce the effects of variation in microclimate along and across the tunnel. The positions of entire blocks were changed, and the locations of pots within each block were re-randomized.

The pots were not watered after 10th August 1986. This arrested plant growth and seed production. Mustard has an indeterminate growth form and would otherwise have continued to flower indefinitely. Pots were harvested between 26th August and 16th September 1986. The numbers of surviving plants of each species in each pot were recorded, and parts of plants bearing seeds were bagged and stored. Seeds were separated and counted for each species in each pot at a later date.

Statistical Analysis.

Difference equation models (Chapter 2) of the relationship between seed sown and seed harvested per unit area were fitted to the data using a least squares non-linear regression technique. Difference equations of the Hassell and Law and Watkinson types were fitted. The Hassell models in this case are:

wheat : $$N_{t+1w} = \frac{\lambda_w \ N_{tw}}{(1 + a_w(N_{tw} + \alpha_w \ N_{to} + \beta_w \ N_{tm}))^{bw}}$$

oats : $$N_{t+1o} = \frac{\lambda_o \ N_{to}}{(1 + a_o(N_{to} + \alpha_o \ N_{tw} + \beta_o \ N_{tm}))^{bo}}$$

mustard : $$N_{t+1m} = \frac{\lambda_m \ N_{tm}}{(1 + a_m(N_{tm} + \alpha_m \ N_{tw} + \beta_m \ N_{to}))^{bm}}$$

The Law and Watkinson models are :

wheat : $$N_{t+1w} = \frac{\lambda_w \ N_{tw}}{1 + N_{tw}b1w + N_{to}b2w + N_{tm}b3w}$$

oats : $$N_{t+1o} = \frac{\lambda_o \ N_{to}}{1 + N_{to}b1o + N_{tw}b2o + N_{tm}b3o}$$

mustard : $$N_{t+1m} = \frac{\lambda_m \ N_{tm}}{1 + N_{tm}b1m + N_{tw}b2m + N_{to}b3m}$$

For those densities at which either transplanting or thinning was carried out, germination rates estimated from the lower densities were used to calculate the mean density which would have been sown in order to achieve that seedling density. The models were fitted to various transformations of the data set in order to choose a transformation which ensured homogeneity of error variance. Log_{10} transformation proved overall to give the best distributions. Non-linear regression and all statistical tests were carried out using the SAS package (SAS, 1985).

A number of statistics relating to the goodness of fit of the model are available (Brook and Arnold, 1985). One of the most commonly used is the coefficient of determination, R^2:

$$R^2 = \frac{\text{regression sum of squares}}{\text{total sum of squares}}$$

This coefficient indicates the proportion of the variation in the uncontrolled variable explained by the model. The model is a good fit if R^2 approaches 1. However, the value of R^2 depends in part upon the sample size and the number of parameters to be estimated, and will always be at least a slight overestimate. An adjusted value is available, where n is the number of observations and k is the number of predictor variables, as follows:

$$\text{adj } R^2 = \frac{(R2 - k/n-1)\,(n-1)}{n - k - 1}$$

When n is much larger than k, however, the difference between R^2 and adj R^2 is very small.

Two F-tests may be used to assess the fit of the model. The first uses

$$F = \frac{\text{regression mean square}}{\text{error mean square}}$$

The null hypothesis is that the proportion of the variance explained by the model is no greater than that remaining. If the F-value is sufficiently large, the null hypothesis can be rejected, and the model can be considered feasible, though not necessarily optimal. The second F-test uses the concept of pure error and is applicable only where each treatment is replicated.

$$\text{Pure error sum of squares} = \sum_{c}^{i} \sum_{c}^{j} (y_{ij} - y_i)^2$$

where y values are observed values for the i^{th} treatment with j replicates: y_{ij} is is an observed value, y_i is the mean value for the particular treatment. It is an estimate of the amount of error inherent in the data. The error sum of squares for the regression can be partitioned into that inherent in the data and that due to the lack of fit of the model:

Lack of fit sum of squares = error sum of squares - pure error sum of squares

$$\text{Then,} \quad F = \frac{\text{lack of fit mean square}}{\text{pure error mean square}}$$

When this statistic is not significantly different from one, the model is accepted as being a good description of the underlying relationship. If F exceeds this value, then the model is not the best possible although it may fit

the data reasonably well. Both these F tests were applied to the fitted models.

The dynamical behaviour of the fitted models was explored using computer simulation. The equations for each species were applied to a wide range of initial mixture compositions for many generations. No statistics are available which can give estimates of the variances of the predictions of the entire model. To discover how much the conclusions of these simulations depend upon the precise parameter values obtained from the regression, parameter estimates were varied. This involved varying parameter estimates widely within their 95% confidence limits, and repeating the simulation exercise for each change in parameterization. For the Hassell model each parameter in turn was increased to its 95% confidence limit in all 3 species together, λ and a being increased together since their estimates were highly correlated. In addition, b was decreased to its lower 95% limit, and a and b terms were adjusted in various ways in an attempt to maximize the effect on the outcome. For the Law and Watkinson model, λ was raised to its 95% confidence limits. Further, interaction terms were raised or lowered in all 3 species to favour each species in turn.

Results.

Ideally, experimental data would be presented graphically before the results of model fitting were given. However, a complete representation would require a series of 4-dimensional graphs with densities of each species as 3 axes and yield of one of the species as the fourth. This would be impossible, so monoculture data alone are presented in this form. Figure 1* shows graphs of seed harvested against seed sown on $\log_{10}$ axes. This

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* In Figure 1, as in other figures in this thesis, axes are labelled on one graph only. These labels also apply to the axes of the other graphs in the figure.

Figure 1. Yield / density relationships in monocultures. The 1:1 lines link points at which equal numbers are sown and harvested.

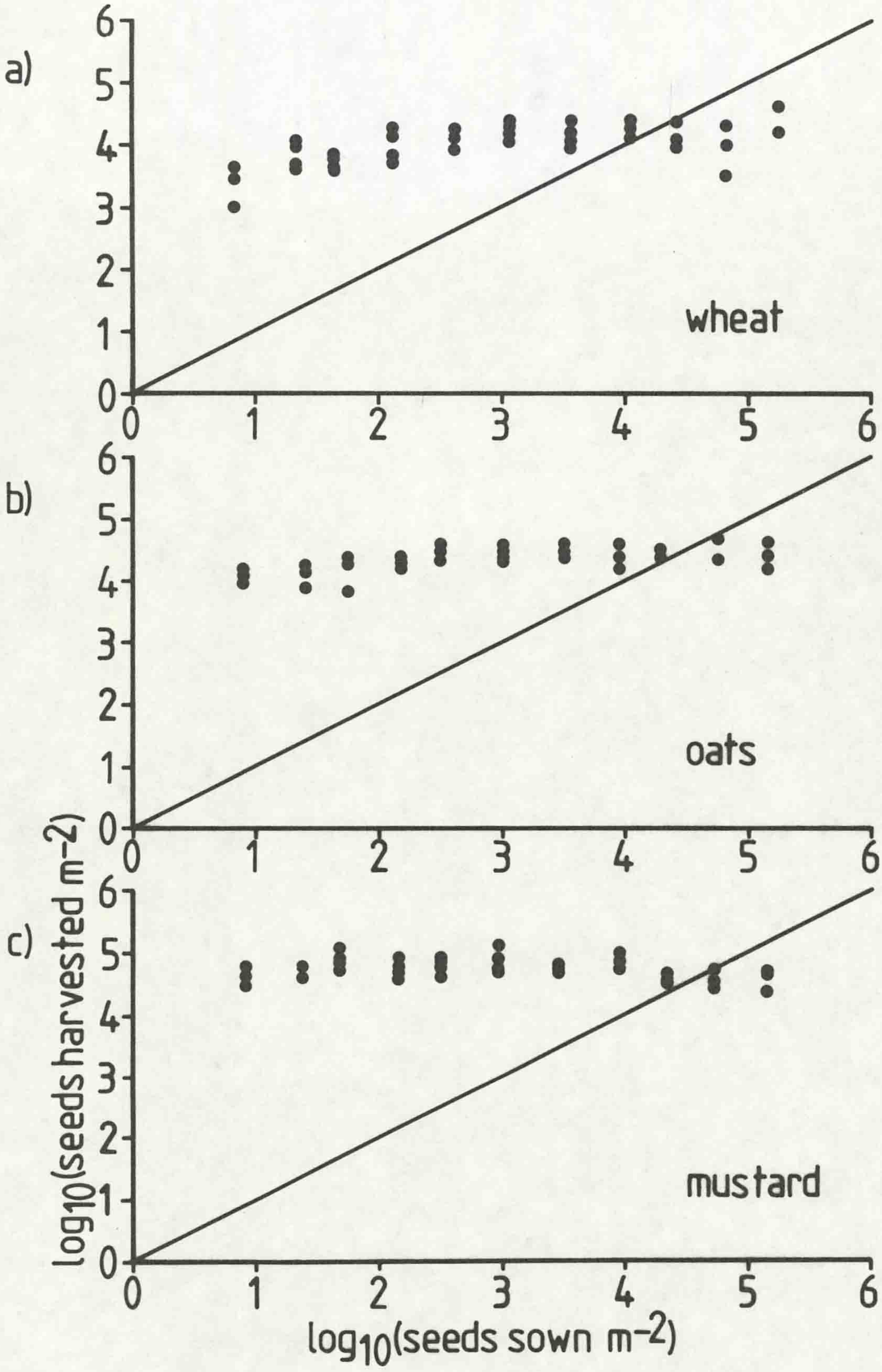


Figure 2. Fecundity / density relationships in monocultures.

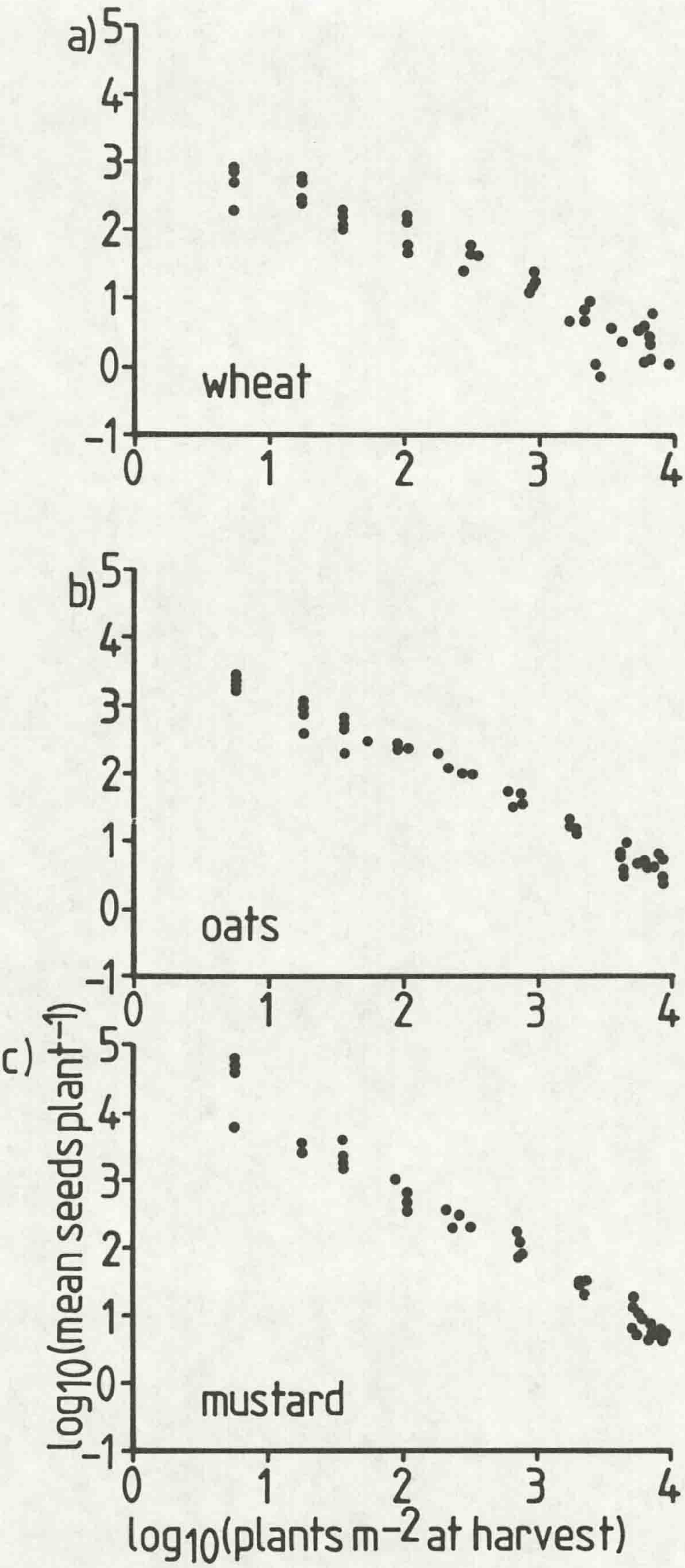
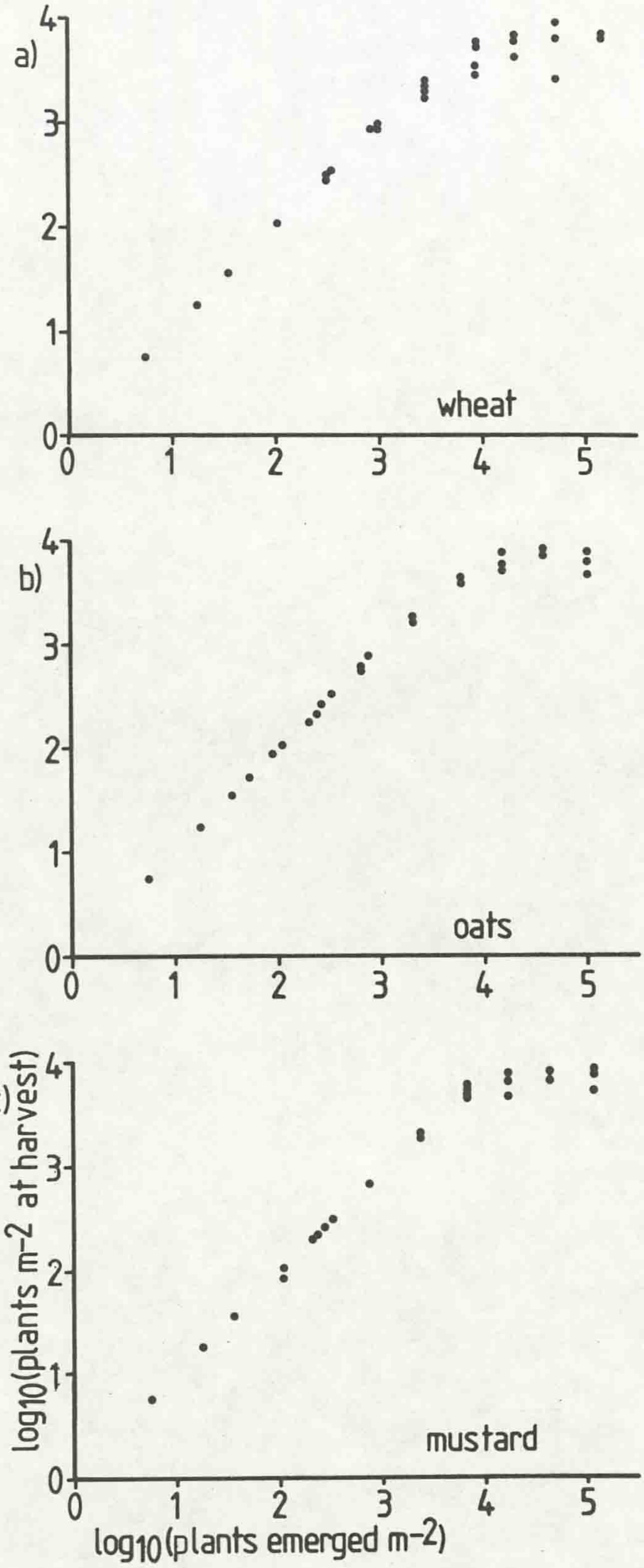


Figure 3. Survivorship / density relationships in monocultures.



relationship is of primary importance in population dynamics since it relates density in one generation to that in the next. Over quite a large proportion of the density range, the law of constant final yield (Kira *et al.*, 1953) appears to hold more or less true. There is some evidence of curvature in the data at lower densities: this is most striking in the wheat data. The lines of data points cross the 1:1 line in each case. This shows that at least in monoculture, sown densities were high enough to reach the equilibrium density. This suggests that models fitted to the data are likely to give reliable estimates of equilibrium population levels.

The seed-seed density relationship across one generation is potentially the result of both density dependent mortality and fecundity. Figure 2 shows mean seed yield per plant plotted against plant density at harvest. There is a clear inverse linear relationship when plotted on logarithmic axes, showing that fecundity was density dependent over almost the whole density range. Only in wheat is there evidence of a tailing-off at low densities, suggesting that the lowest densities are in a range where fecundity becomes independent of density. Figure 3 shows mortality as plants at harvest against plants emerging. Plotted on $\log_{10}$ axes, data points are close to the 1:1 line at lower densities, indicating that there was little or no mortality over this part of the density range. At higher densities the data tail off towards the horizontal: a horizontal line indicates complete compensation by mortality for increases in sowing density.

These results from monocultures support the view that at very low densities yields of individuals and stands are independent of density. As density increases, it is at first compensated for by the plasticity of individual plants (density dependent fecundity), but at very high densities the death of plants becomes another compensatory factor (density dependent mortality). This graphical treatment cannot, however, give a full picture of competitive effects in mixtures. For this, fitted models must be examined.

The parameters in each of the fitted models are shown in Tables 1 and 3. The standard errors of some of the estimates are very large, particularly those of λ and a in the Hassell model. This is largely because very low density treatments from which the best estimates of λ would be obtained are absent. If much significance were to be placed on the values of individual parameters rather than the behaviour of the whole models, this would be a serious problem. However, the parameter estimates are all correlated to some degree (Tables 2 and 4) and the correlations between λ and a estimates are especially high. Hence, the high standard errors of λ and a probably reflect the fact that they can <u>together</u> vary a great deal without much affecting either the regression sum of squares or the behaviour of the whole model. This is likely to be the explanation for the large difference in λ estimates for wheat between the Hassell and Law and Watkinson models.

The values of b in the Hassell model have particular biological significance at high total densities. When b=1, a condition of constant final yield is approached. When b<1, yield always increases as ($N_{1t} + \alpha N_{2t} + \beta N_{3t}$) increases. When b>1, yield increases to a maximum and then declines again as this term increases. Both b=1.40 for wheat and b=0.892 for oats significantly depart from b=1 (t-test, $p<0.05$). The implication is that in these three species mixtures only mustard exhibits constant final yield.

Values of α and β in the Hassell model are equivalence coefficients representing the number of plants of a second species which have the same effect on the yield of a first species as one individual of the first species (see Chapter 2). The effect on wheat of a mustard plant is greater than that of an oat plant, which is in turn greater than that of a wheat plant. For oats, a wheat plant has only the effect of 0.7 oat plants, whilst mustard has the effect of 9 wheat plants. The effect on mustard of an individual of either cereal is much smaller than that of a mustard plant. Hence, an order of aggressiveness can be written:

Table 1. Parameter estimates and (in brackets) their asymptotic standard errors in best-fit Hassell models.

Parameter	Wheat	Oats	Mustard
λ	227 (70.8)	4570 (7160)	11800 (5360)
a	0.00372 (0.00171)	0.362 (0.720)	0.164 (0.0870)
b	1.40 (0.0869)	0.892 (0.0336)	1.04 (0.0225)
α	4.49 (1.20)	0.683 (0.275)	0.172 (0.0451)
β	9.96 (2.25)	9.31 (1.71)	0.0795 (0.0412)

Table 2. Asymptotic correlation matrices of parameters in best-fit Hassell models. In each box, values (from top to bottom) for wheat, oats and mustard are shown.

	λ	a	b	α	β
λ	1.0				
	1.0				
	1.0				
a	0.80	1.0			
	0.99	1.0			
	0.98	1.0			
b	-0.44	-0.77	1.0		
	-0.59	-0.67	1.0		
	-0.56	-0.70	1.0		
α	-0.12	-0.48	0.20	1.0	
	-0.17	-0.16	-0.02	1.0	
	-0.14	-0.21	0.17	1.0	
β	-0.12	-0.45	0.10	0.64	1.0
	-0.27	-0.30	-0.19	0.38	1.0
	-0.12	-0.20	0.23	0.10	1.0

Table 3. Parameter estimates and (in brackets) their asymptotic standard errors in best-fit Law and Watkinson models.

Parameter	Wheat	Oats	Mustard
λ	10200 (2870)	6330 (1210)	72500 (8820)
b_1	0.972 (0.0440)	0.824 (0.0291)	1.04 (0.0165)
b_2	1.17 (0.0542)	0.710 (0.0665)	0.767 (0.0448)
b_3	1.30 (0.0494)	1.09 (0.0330)	0.535 (0.142)

Table 4. Asymptotic correlation matrices of parameters in best-fit Law and Watkinson models. In each box, values (from top to bottom) for wheat, oats and mustard are shown.

	1.0			
λ	1.0			
	1.0			
	0.83	1.0		
b_1	0.84	1.0		
	0.93	1.0		
	0.82	0.62	1.0	
b_2	0.60	0.31	1.0	
	0.60	0.45	1.0	
	0.87	0.69	0.69	1.0
b_3	0.88	0.72	0.50	1.0
	0.58	0.45	0.22	1.0
	λ	b1	b2	b3

Table 5. Goodness of fit of the models.

R^2 is the coefficient of determination.

adj R^2 is the adjusted coefficient of determination.

F_1 is the F value for the comparison of regression / total error, where rejection of the null hypothesis as fitting well.

MS(LF) is the lack of fit mean square.

F_2 is the F value for the lack of fit / pure error comparison, where rejection of the null hypothesis leads to rejection of the model as giving optimal fit to the data.

	Hassell model		Law and Watkinson model	
Wheat	R^2 = 0.980		R^2 = 0.979	
	adj R^2 = 0.979		adj R^2 = 0.978	
	F_1 = 1890	***	F_1 = 2208	***
	MS(LF) = 0.343		MS(LF) = 0.395	
	F_2 = 1.78	*	F_2 = 2.05	*
Oats	R^2 = 0.993		R^2 = 0.992	
	adj R^2 = 0.993		adj R^2 = 0.992	
	F_1 = 5270	***	F_1 = 6150	***
	MS(LF) = 0.102		MS(LF) = 0.126	
	F_2 = 1.33	NS	F_2 = 1.13	NS
Mustard	R^2 = 0.998		R^2 = 0.998	
	adj R^2 = 0.998		adj R^2 = 0.998	
	F_1 = 24800	***	F_1 = 30600	***
	MS(LF) = 0.0458		MS(LF) = 0.0468	
	F_2 = 1.55	*	F_2 = 1.58	*

Significance levels for F-tests:

*** rejection of null hypothesis at 99.9% level.

** rejection of null hypothesis at 99% level.

* rejection of null hypothesis at 95% level.

NS acceptance of null hypothesis at 95% level.

wheat < oats < mustard.

In the Law and Watkinson model, values of b_2 and b_3 relate to equivalence, though less simply. Again, however, values less than 1 mean that an individual of the second species has less effect than one of the first, and values greater than 1 mean the opposite. Fitted b_2 and b_3 values suggest the same order of aggressiveness of individuals. It is important to note that these do not predict the outcome of competition. All the parameters interact in this.

Goodness of fit statistics are shown in Table 5 for each model fitted to data from each species. R^2 and adjusted R^2 values all exceed 0.97 indicating that a very large proportion of the variation in the data is explained by the model. The first F-test, comparing regression mean square and total error mean square, confirms this: in all cases the null hypotheses are rejected at the 99.9% level. Both models are feasible for each species. However, in the second F-test comparing lack of fit and pure error mean squares, the null hypotheses of no lack of fit are rejected for both models in wheat and mustard. Hence, there are no substantial grounds to favour one model over the other, and there is evidence that for wheat and mustard, while both models provide adequate fit, better models might be found. This problem is discussed later in this chapter, but it must be remembered that simplification is the essence of modelling. Adequacy is the aim, perfection being both unnecessary and unattainable.

Figures 4 and 5 show some examples of simulations of community dynamics in the wheat/oat/mustard mixture, obtained by iteration of the models. In each figure, the four graphs a) - d) show simulations of dynamics from four initial community compositions. The predictions of the two types of model are very similar. Regardless of initial composition, mustard becomes dominant within very few generations, wheat and oats declining towards extinction. Equilibrium population densities for mustard are 50200 seeds m^{-2}

(Hassell model) and 47100 seeds m^{-2} (Law and Watkinson model). In binary mixtures containing mustard, mustard again becomes dominant. In wheat/oats mixtures, oats drives wheat to extinction, equilibrium oats densities being 35000 (Hassell) and 41100 (Law and Watkinson) seeds m^{-2}. Monoculture equilibrium densities for mustard and oats are as in mixtures; in wheat they are 12700 (Hassell) and 13310 (Law and Watkinson) seeds m^{-2}.

Simulations also demonstrate the way in which equilibrium is reached. This may be either by convergent oscillations or monotonically. When maximum yield occurs at a higher density than the equilibrium density, approach can only be monotonic. Convergent oscillations can occur when maximum yield is obtained at less than the equilibrium density, although monotonic approach and chaotic behaviour can also occur under this condition for some combinations of parameter values. In the Hassell model these conditions mean that b must exceed 1 and λ must lie in a certain range, below which there is monotonic approach to equilibrium and above which there is chaotic behaviour (Chapter 2, equations 30). Simulation shows that the Hassell model predicts that in monoculture (Figure 6) and in mixtures in which the species becomes dominant, wheat reaches equilibrium by convergent oscillations, mustard by convergent oscillations of a much smaller amplitude, and oats monotonically. The Law and Watkinson model predicts convergent oscillations, again of small amplitude, for mustard only.

The interpretation of these data by fitting difference equation models depends entirely on the least squares regression technique. Whilst these models give the best fit, it is possible that others, fitting nearly as well, might seriously alter the biological predictions. This would severely limit the usefulness of the models. However, the changes in parameterization based on 95% confidence limits of parameter estimates made little difference to the

Figure 4. Simulations of community dynamics based on Hassell models (Table 1).

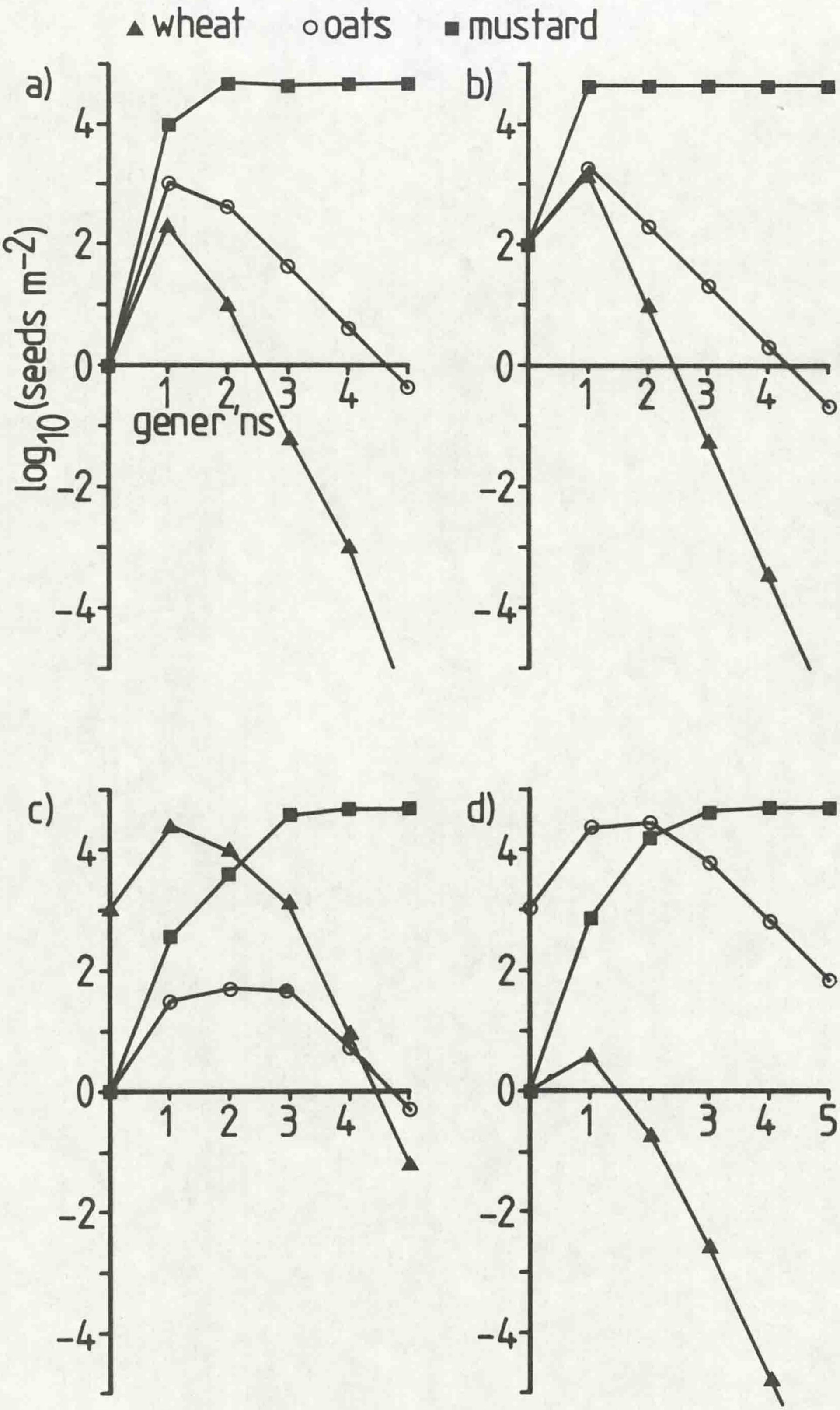


Figure 5. Simulations of community dynamics based on Law and Watkinson models (Table 3).

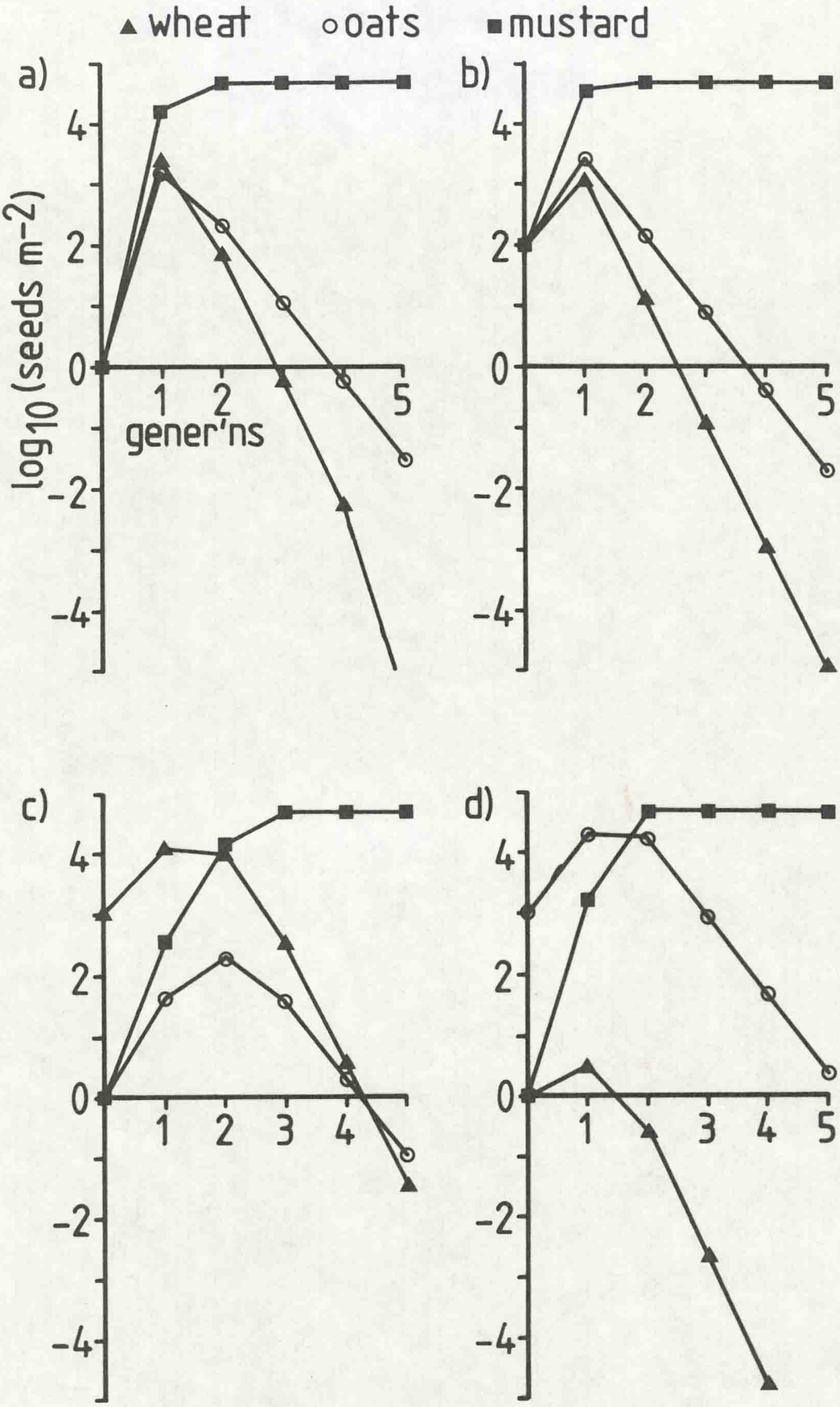
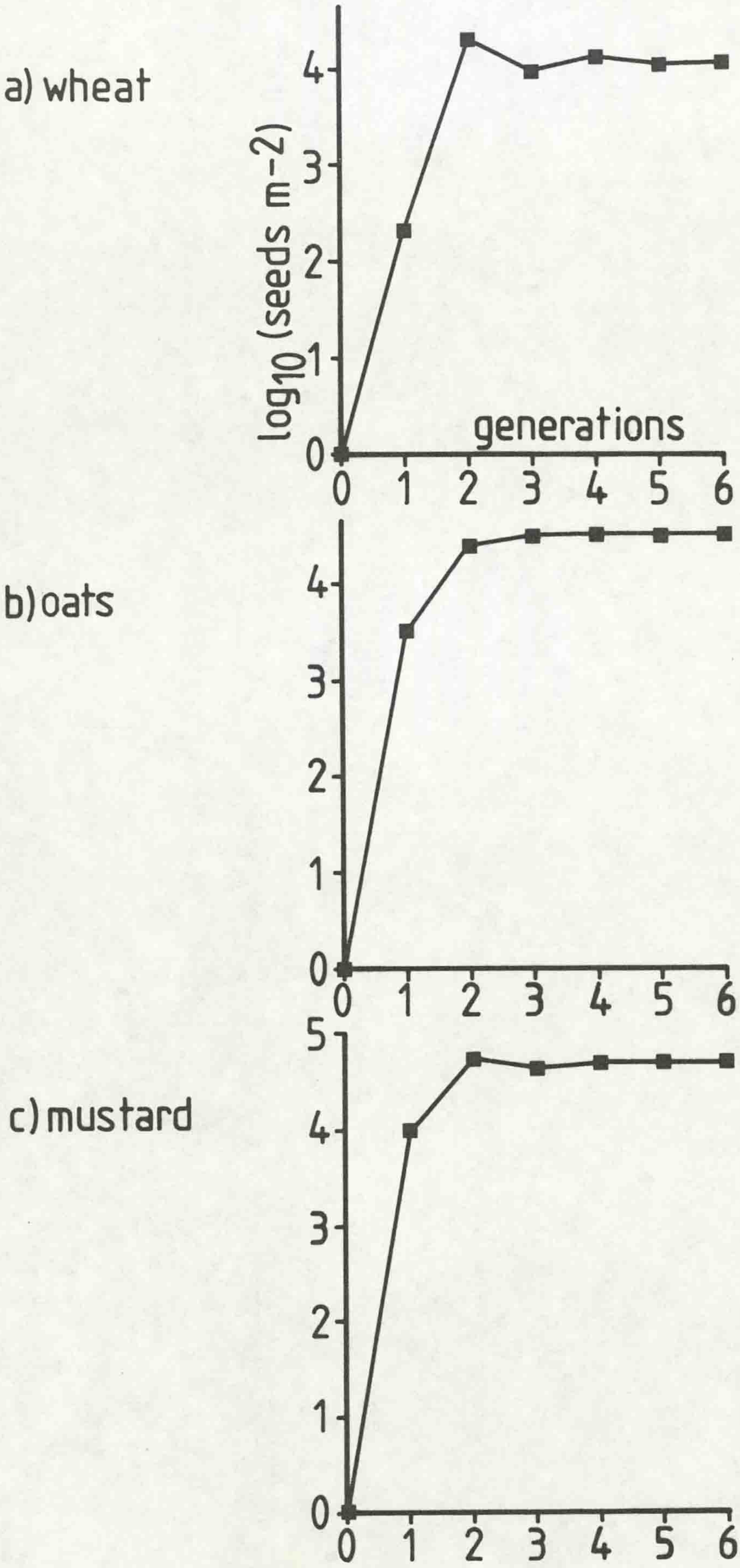


Figure 6. Simulations of monoculture dynamics based on Hassell models (Table 1).



outcome of simulations. In no case did the qualitative nature of the equilibria in either model change, although the way in which equilibrium was reached was more sensitive to these changes. The quantitative natures of equilibria were changed, though equilibrium seed density was never more than doubled or less than halved.

Discussion.

a). Methodological Discussion.

This study appears to be the first in which competition in mixtures of more than two species has been studied over a wide range of both densities and frequencies. Models have been fitted to the entire range of data. This makes conclusions more widely valid than those drawn from additive or replacement series experiments. The cost of this generality is in the size of the experiment, which took approximately 1500 man-hours, excluding analysis, to complete. The size of this type of experiment increases geometrically with the number of species involved. This limits the applicability of the approach to systems of relatively few species.

Carrying out this type of experiment in pots rather than in the field has several consequences. Firstly, it allows a more closely controlled environment, tending to reduce experimental error, at the expense of relevance to the field situation. The object of this experiment was primarily to assess the usefulness of this approach in an annual plant community of three species, rather than to study a particular community as found in nature. Hence, the pot system was preferable. The second consequence is that in pots the lower limit to the density range is restricted by pot size. On the other hand, whilst larger plots are possible in the field, it is harder to achieve really high densities since the quantities of seed required would be enormous. This problem of pots was partially overcome by the use of some

large pots. Whilst maximum attainable yield of single plants did not appear to have been reached at the lowest densities, there was sufficient curvature in the Nt+1/Nt data for the models to fit well.

Replication is not an essential feature of experimental designs when the object is to establish a relationship between two variables by regression. The more data available, the better the estimate of the model parameters is likely to be, but several replicates at fewer points are not necessarily preferable to more, unreplicated, points. The value of replication in this experiment is that it enables significance tests for the lack of fit of the model to be used. The estimates of wheat, oats and mustard yields are taken from the same pots, as is usual in this type of experiment. This means that the estimates are statistically dependent. Statistical independence can be achieved by harvesting only one species per pot (Law and Watkinson, 1987). To achieve the same number of data, this would require a much larger experiment, which would have been impractical in this study. However, since the models are being incorporated into a predictive model of community dynamics rather than subjected to critical species comparisons, this criticism is not too serious.

There are no substantial grounds for favouring either the Hassell or the Law and Watkinson model in this study. Their predictions of community dynamics are remarkably similar, as are the goodness of fit statistics. Law and Watkinson (1987) compared these models (as well as six others, considered inferior to these) and considered that the Law and Watkinson model was superior because there was no significant lack of fit for either of the species that they used: the Hassell model gave significant lack of fit for one species. In the present study, there was significant lack of fit for two out of three species for both models. It might appear that the models fit Law and Watkinson's dune annual data better than these crop data: this is not, however, the case. Such a conclusion would come from considering the

second F-test in isolation. This test compares lack of fit mean square with pure error mean square. When experimental data are 'cleaner', with a lower pure error mean square, less lack of fit is required for the lack of fit to be significant. Lack of fit mean square is the true measure of lack of fit. Law and Watkinson's values of lack of fit mean square can be calculated for *Vulpia fasiculata* (Forskål) Samp. as 0.0930 (Hassell model) and 0.100 (Law and Watkinson model) and for *Phleum arenarium* L. as 0.606 (Hassell) and 0.433 (Law and Watkinson). In the present study, values for mustard, oats and wheat were 0.0458, 0.102, 0.343 (Hassell model) and 0.0468, 0.126, 0.395 (Law and Watkinson model). The absence of significant lack of fit in the dune annual study is due to a higher background of pure error against which the lack of fit was being observed.

There is, then, no reason to favour the Law and Watkinson model on the basis of lack of fit. In all species in this experiment and in one of Law and Watkinson's two species, the Hassell model provides a slightly better fit. Even though it contains one more parameter, the Hassell model is simpler to visualize, easier to interpret biologically, and is analytically tractable.

b) Biological Discussion.

Whichever model is favoured, the conclusion must be that under these conditions this three species mixture moves rapidly towards a mustard monoculture over generations. Mustard populations increase at the expense of wheat and oats due to both higher intrinsic rate of increase (λ) and greater aggressiveness (α and β in the Hassell model). One factor which might favour mustard is germination time. It is frequently observed (eg Ross and Harper, 1972) that relatively early germination of an individual in a population, or a species in a mixture, can greatly increase its yield, at least when light is the limiting factor (Wilson, 1988). Mustard emergence was

about one week earlier than that of wheat and oats, giving it a "head start" in capture of space, at least above ground. If this is the basis of the competitive superiority of mustard, the advantage conferred must be more than enough to counter the advantage which its smaller seeds may provide (Black, 1958; Gross, 1984), although their small size necessitated shallower sowing which can itself confer an advantage (Abul-Fatih and Bazzaz, 1979).

Mustard also has a potential advantage due to its growth form. The mustard stem grows vertically from the start, whilst wheat and oat stems remain very short, with upwardly angled leaves, during the earlier stages of growth. This allows mustard pre-emptive consumption of much of the light resource.

The timing of harvest in competition experiments can affect the outcome (Connolly, 1986). Plants with a determinate growth form die after a discrete flowering period, whilst indeterminate species continue to flower indefinitely. In a mixture of determinate and indeterminate species, the longer the growth period, the more the indeterminate species will be favoured in the final yield. Mustard has an indeterminate growth form, but it probably did not gain much advantage from this since the experiment was dried out and harvested as soon as wheat and oat seed was ripe.

It is important to note that the conclusions of this experiment should not be extended to other conditions. There is no evidence from the experiment alone to suggest how far conditions could be altered before the outcome became qualitatively different.

Chapter 4.

The Effect of a Herbicide on Competition Between Three Crop Species.

'Whether the swallows and house-martins return in the same exact numbers annually is difficult to say..... but it is apparent.....that the numbers returning bear no manner of proportion to the numbers retiring.'

Gilbert White.

Introduction.

Community dynamics are determined by density dependent competitive effects as well as by environmental influences. The approach taken in this study, as discussed in Chapter 1, is to model competitive processes as the driving force in community dynamics. Environmental factors are seen as modifiers of these processes. One type of environmental perturbation might restrict the growth of, or remove part of one population within a community during the growing season. Such perturbations include selective grazing, disease and the application of selective herbicides.

Chapter 3 described a competition experiment between three crop species in the absence of any such perturbation. The experiment described in this

chapter concerns a more complex and realistic situation: the outcome of competition in the same three species system is compared in the presence and absence of a perturbing factor.

Herbicides, being imposed by man, are convenient for the study of this type of effect. Moreover, they are a particularly important class of perturbing influences in agroecosystems. An experiment to determine the effect of a herbicide on a mixture would ideally consist of a design in which both total density and relative frequency are varied, repeated with and without herbicide. No such experiments have been reported, but in a related type of study using a mixture of barley (*Hordeum vulgare* L.), white mustard (*Sinapis alba* L.) and wild oats (*Avena fatua* L.), Haizel and Harper (1973) measured the effect of removing either one or two species from replacement series designs after three weeks' growth. This is similar to a perturbation by herbicide in that there is scope for the unaffected species to be released from competition, but different in that there is no scope for recovery by the affected species. The results provided interesting evidence that the concept of an order of aggressiveness amongst a group of species is not always valid. However, the results could not be generalized beyond the densities used, and could not be used to generate predictive models of changes in mixture composition.

This chapter describes an experiment using three crop species in a design in which both density and frequency are varied widely, with and without herbicide application. Predictive models of seed yield of each species in terms of sowing densities of all three species are generated, and their validity is assessed.

Materials and Methods.

The species used in this experiment were spring wheat (*Triticum aestivum* L. cv Bounty), spring oats (*Avena sativa* L. cv Dula) and white mustard (*Sinapis alba* L.). The same seed stocks as in the previous experiment (Chapter 3) were used. The experiment was performed in an unheated polythene tunnel at the University of Liverpool Botanic Gardens, Ness, Cheshire. Plants were grown in pots of area 0.056m^2 in a John Innes compost with only half the added fertilizer of J.I. No.1 (780 g m^{-3}). Wheat and oats were sown at a depth of 50 mm, mustard at a depth of 5 mm.

The design was based upon densities of each species of 0, 1, 6, 36, 216 and 1296 seeds per pot (0 to 23000 seeds m^{-2}). These densities were adjusted for each species according to the results of a viability test giving results of 100% for wheat, 50% for oats and 90% for mustard. These densities were combined in all possible ways, taking one density of each species, resulting in a wide range of monocultures, binary mixtures and ternary mixtures. In addition, a monoculture density of one plant in larger pots of area 0.30 m^2 was sown. The ratio of soil volume to soil surface area was kept constant in the two pot sizes. The monocultures and some ternary mixtures were replicated but there was no complete replication. This lack of replication was justified because no comparison of treatments was to be made. Analysis was primarily by regression which does not require replicated points. Lack of replication did, however, mean that it was impossible to estimate pure error. For every mixture set up, a pot was sown with an identical mixture which was later treated with a herbicide. Pots were laid out randomly, sprayed and unsprayed together.

Seeds were sown into dry soil over three days, then all were initially watered on 10th March,1987. Thereafter, pots were watered daily, and in the later stages of the experiment the fungicides bupirimate and triforine were

applied prophylactically at fortnightly intervals, each at a concentration of 41mg l^{-1}. Strings were tied to canes around each pot to prevent lodging.

Seedlings were counted soon after germination. In any pot in which 1 or 6 seedlings of a species were expected, transplants were made from spare pots or surplus plants were removed, to correct for variation in germination rates.

Pots to be sprayed were separated on 15th April 1987. The herbicide 2,4-dichlorophenoxyacetic acid (2,4-D), which selectively affects dicotyledonous species, was applied at a rate of 0.5 ml m^{-2} in 56 ml m^{-2} water. Rates of 1.4 to 14 ml m^{-2} are recommended. This relatively low dose was chosen as a result of a dose-response trial carried out only two weeks ahead of the main experiment in order to minimize any effect of seasonal variation in temperature. The dose used was chosen as severely checking growth of mustard (canopy height of sprayed mustard monocultures was only $^2/_3$ that of unsprayed controls after 2 weeks), but resulting in little mortality after 2 weeks. After the herbicide had dried onto the leaves, all pots were rerandomized in order to reduce the effects of microclimate variation along and across the tunnel.

The pots were not watered after mid July 1987, to halt seed production in all pots simultaneously. The experiment was harvested between 22nd July and 17th August 1987. The numbers of surviving plants of each species in each pot were recorded and parts of plants bearing seeds were bagged and stored. Seeds were separated and counted for each species at a later date.

Statistical Analysis.

Difference equation models of the Hassell and Law and Watkinson types (Chapter 2) of the relationship between seed sown to seed harvested per

unit area were fitted to the data using a least squares non-linear regression technique as previously described. The Hassell models in this case are:

wheat : $$N_{t+1w} = \frac{\lambda_w \ N_{tw}}{(1 + a_w(N_{tw} + \alpha_w \ N_{to} + \beta_w \ N_{tm}))^{bw}}$$

oats : $$N_{t+1o} = \frac{\lambda_o \ N_{to}}{(1 + a_o(N_{to} + \alpha_o \ N_{tw} + \beta_o \ N_{tm}))^{bo}}$$

mustard : $$N_{t+1m} = \frac{\lambda_m \ N_{tm}}{(1 + a_m(N_{tm} + \alpha_m \ N_{tw} + \beta_m \ N_{to}))^{bm}}$$

The Law and Watkinson models are :

wheat : $$N_{t+1w} = \frac{\lambda_w \ N_{tw}}{1 + N_{tw}b1w + N_{to}b2w + N_{tm}b3w}$$

oats : $$N_{t+1o} = \frac{\lambda_o \ N_{to}}{1 + N_{to}b1o + N_{tw}b2o + N_{tm}b3o}$$

mustard : $$N_{t+1m} = \frac{\lambda_m \ N_{tm}}{1 + N_{tm}b1m + N_{tw}b2m + N_{to}b3m}$$

For those densities at which either transplanting or thinning was carried out, germination rates estimated from the lower densities were used to calculate the mean density which would have been sown in order to achieve that seedling density. These models were fitted independently to data from sprayed and unsprayed pots. Various transformations of the data were tried in order to choose one which ensured homogeneity of error variance. Log_{10} transformation proved, overall, to give the best distributions. Non linear regression and all statistical tests were performed using the SAS package (SAS 1985).

Goodness of fit of the models was assessed by R^2, adjusted R^2 and an F test comparing regression mean square and error mean square (Brook and Arnold,1985). The F test for significance of lack of fit could not be used because the experiment was not fully replicated and so pure error could not be estimated.

The dynamical properties of the fitted models were explored by computer simulation. The equations for each species were iterated, taking a wide range of initial mixture compositions. It is important to discover how much the conclusions of these simulations depend upon the precise parameter values obtained in the regression. No statistics are available which can give estimates of the variance of the predictions of the entire model. Hence, this was investigated by widely varying parameter estimates within their asymptotic 95% confidence limits, and repeating the simulation exercise for each change in parameterization. For the Hassell model, each parameter was increased in turn to its upper 95% limit, λ and a being raised together, and α and β terms were adjusted in various ways in an attempt to maximize the effect on the outcome. For the Law and Watkinson model, λ was raised to its upper 95% confidence limit and interaction power terms were raised or lowered in all three species to favour each species in turn.

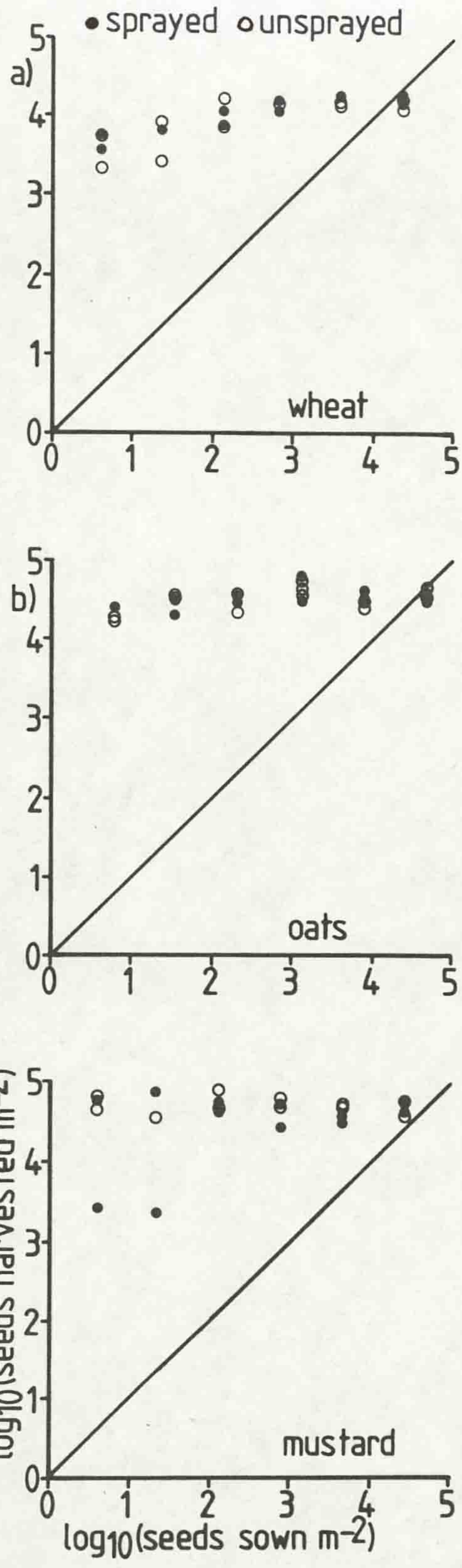
A model for a species experiencing control in the presence of two uncontrolled species (equation 27, Chapter 2) was fitted to the mustard data from sprayed pots. All parameters were allowed to vary. Then the same model was fitted, substituting values of λ, a, α, β and b from the Hassell model for unsprayed mustard, and allowing only Λ to vary.

Results

As in Chapter 3, a complete graphical presentation of the data is not possible since this would require a 4-dimensional graph. Monoculture data alone are presented in this form. Figure 7 shows graphs of seed harvested against seed sown on $\log_{10}$ axes. This is of central importance, relating density in one generation to that in the next. The only suggestion of a herbicide effect on mustard at this level comes from the two lowest densities (1 plant per pot in large and normal pots). In each case, one replicate sprayed point is similar to the unsprayed points, whilst the other is many times lower. A possible interpretation is that the herbicide strongly suppresses the growth of some individuals: this can be overcome by compensatory growth of other individuals only if they are present.

This seed-seed density relationship (Figure 7) across one generation may be the result of both density dependent mortality and fecundity. Figure 8 shows mean seed yield per plant plotted against plant density at harvest. This demonstrates that in each species fecundity is varying with density across the whole density range investigated. There is no evidence of a tailing-off at lower densities, suggesting that maximum attainable yield was not, or was only just, reached. The only indication of a herbicide effect on mustard in monoculture is, again, the two low points at the lowest two densities. Figure 9 shows mortality as plants at harvest against plants germinating. These data indicate that there was no obvious effect of the herbicide on mortality. The mortality effects are exactly those seen in the previous year's experiment. Even though the extreme monoculture density was not as high in the present experiment, significant mortality occurred at the highest density. This graphical treatment cannot give a full or rigorous picture of competitive effects in this system. For this, the fitted models must be examined.

Figure 7. Yield / density relationships in monocultures. The 1:1 lines link points at which equal numbers are sown and harvested.



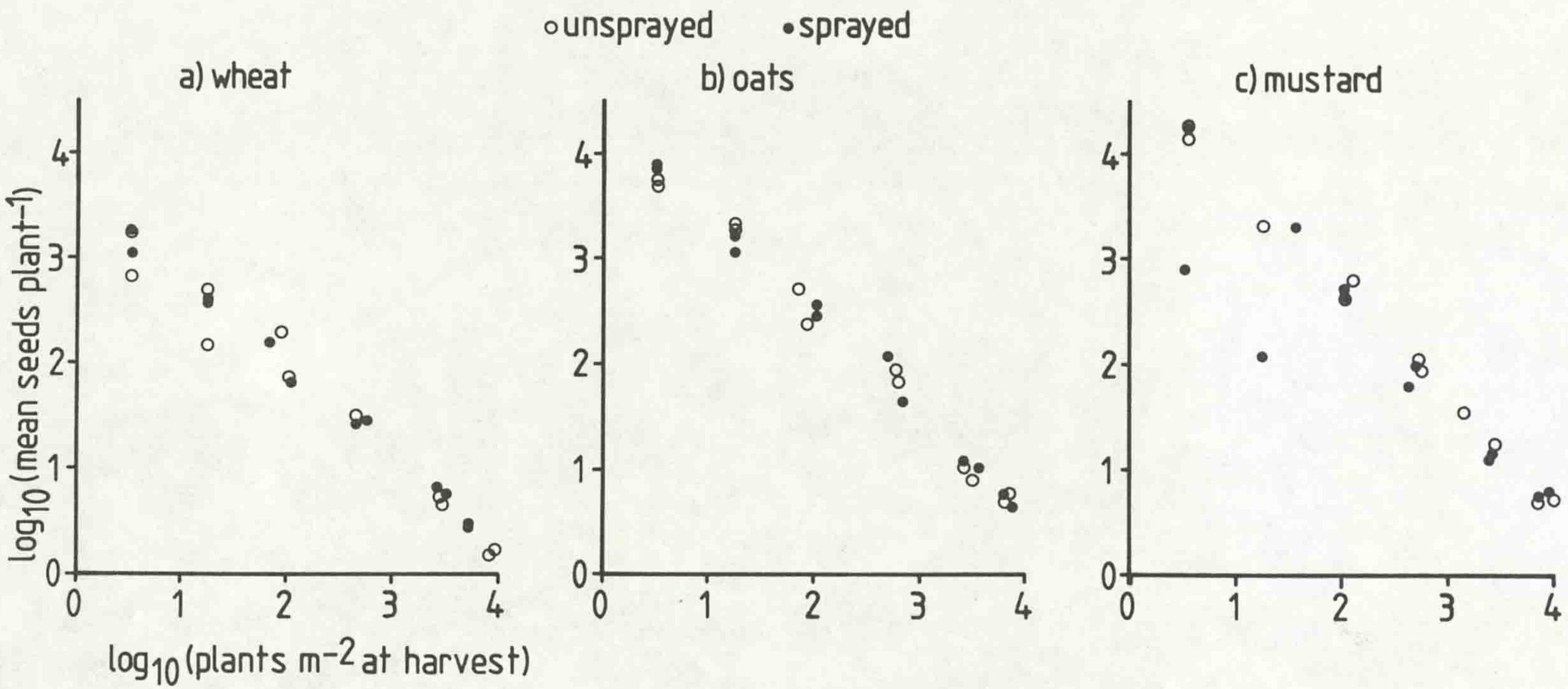


Figure 8. Fecundity / density relationships in monocultures.

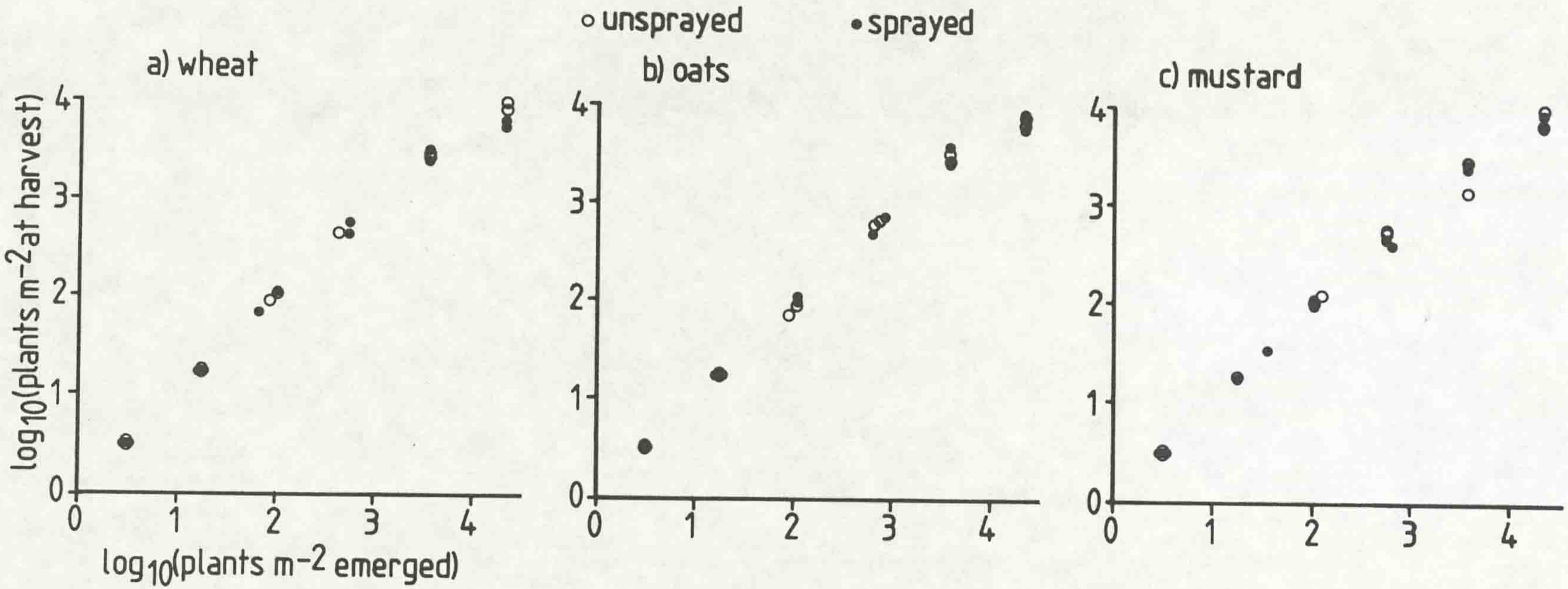


Figure 9. Survivorship / density relationships in monocultures.

Tables 6 and 7 show the parameter values in each of the fitted models. Table 8 shows the goodness of fit of those models. In each case the goodness of fit is statistically significant. Moreover, R^2 values are very high, all exceeding 0.96. However, some of the standard errors of parameter estimates are very large, especially those of λ and a in the Hassell model. All of these exceed the parameter values, by factors of between 1.6 and 46000. This contrasts with the previous year's experiment, in which standard errors of λ and a were mostly smaller than the parameter values, and never more than twice as large. This begins to suggest that less faith should be put in the predictions of the models in the present study. Further evidence for this comes from the results of the simulation and parameter variation exercises. Figures 10 and 11 show some examples of simulations of community dynamics in the wheat/oats/mustard mixture, with and without herbicide, obtained by iteration of the models. In each figure, a) and b) show simulations of dynamics from two initial community compositions in the absence of herbicide, whilst c) and d) show simulations from the same two initial compositions when sprayed with herbicide. Even from the few examples given, it is clear that the Hassell and Law and Watkinson models sometimes give different predictions and that the model predictions can depend upon the initial composition of the mixture. In the absence of herbicide, the predictions of the Hassell model are similar to those of the previous year's experiment, with mustard driving the cereals to extinction and reaching an equilibrium density of 44000 seeds m^{-2}. The competitive balance between wheat and mustard appears to be quite fine, wheat populations declining only slowly. The Law and Watkinson model predicts that from some starting points mustard will rapidly exclude wheat and oats (Figure 11a), reaching an equilibrium density of 45000 seeds m^{-2}, but that from others either wheat (Figure 11b) or oats may drive the other two species to extinction. In the presence of herbicide, the Hassell model predicts that

Table 6. Parameter estimates and (in brackets) their asymptotic standard errors in best-fit Hassell models.

	Unsprayed			Sprayed		
	Wheat	Oats	Mustard	Wheat	Oats	Mustard
λ	62700 (8.33×10^7)	2.48×10^5 (2.04×10^7)	7.69×10^7 (3.6×10^{12})	4590 (10300)	19200* (25800)	55100 (4.28×10^6
a	63.6 (1.22×10^5)	27.3 (2600)	1750 (8.08×10^7)	1.14 (3.18)	0.697* (1.14)	16.4 (1680)
b	0.768 (0.053)	0.890 (0.050)	1.00 (0.0403)	0.850 (0.0315)	0.964* (0.0356)	0.761 (0.102
α	1.33 (0.443)	0.606 (0.226)	0.100 (0.0282)	0.397 (0.0729)	0.599 (0.145)	0.858 (0.633
β	0.691 (0.283)	4.40 (1.140	0.110 (0.0234)	0.769 (0.140)	2.49 (0.377)	0.832 (0.538)

* based on monoculture data only.

Table 7. Parameter estimates and (in brackets) their asymptotic standard errors in best-fit Law and Watkinson models.

	Unsprayed			Sprayed		
	Wheat	Oats	Mustard	Wheat	Oats	Mustard
λ	726 (179)	2970 (877)	41900 (7600)	2020 (308)	5300 (1300)	2650 (1240)
b_1	0.630 (0.0436)	0.720 (0.0466)	0.993 (0.0290)	0.754 (0.0262)	0.799 (0.0377)	0.652 (0.0795)
b_2	0.849 (0.0637)	1.04 (0.0922)	1.10 (0.0659)	1.00 (0.0385)	1.04 (0.0820)	0.702 (0.212)
b_3	0.805 (0.0824)	1.30 (0.0749)	1.12 (0.0470)	1.13 (0.0421)	1.32 (0.0631)	0.995 (0.110)

Table 8. Goodness of fit of the models.

R^2 is the coefficient of determination.

adj R^2 is the adjusted coefficient of determination.

F is the F value for the comparison of regression / total error, where rejection of the null hypothesis as fitting well.

	Hassell model	Law and Watkinson model
Wheat unsprayed	R^2 = 0.987 adj R^2 = 0.987 F = 1860	R^2 = 0.987 adj R^2 = 0.987 F = 2310
Oats unsprayed	R^2 = 0.991 adj R^2 = 0.991 F = 2560	R^2 = 0.987 adj R^2 = 0.987 F = 2310
Mustard unsprayed	R^2 = 0.996 adj R^2 = 0.996 F = 6000	R^2 = 0.996 adj R^2 = 0.996 F = 7610
Wheat sprayed	R^2 = 0.996 adj R^2 = 0.996 F = 6270	R^2 = 0.996 adj R^2 = 0.996 F = 6970
Oats sprayed	R^2 = 0.992 adj R^2 = 0.992 F = 3140	R^2 = 0.992 adj R^2 = 0.991 F = 3610
Mustard sprayed	R^2 = 0.966 adj R^2 = 0.965 F = 680	R^2 = 0.966 adj R^2 = 0.965 F = 864

for all F tests $p<0.001$.

Figure 10. Simulations of community dynamics based on Hassell models (Table 6). a,b) unsprayed; c,d) sprayed.

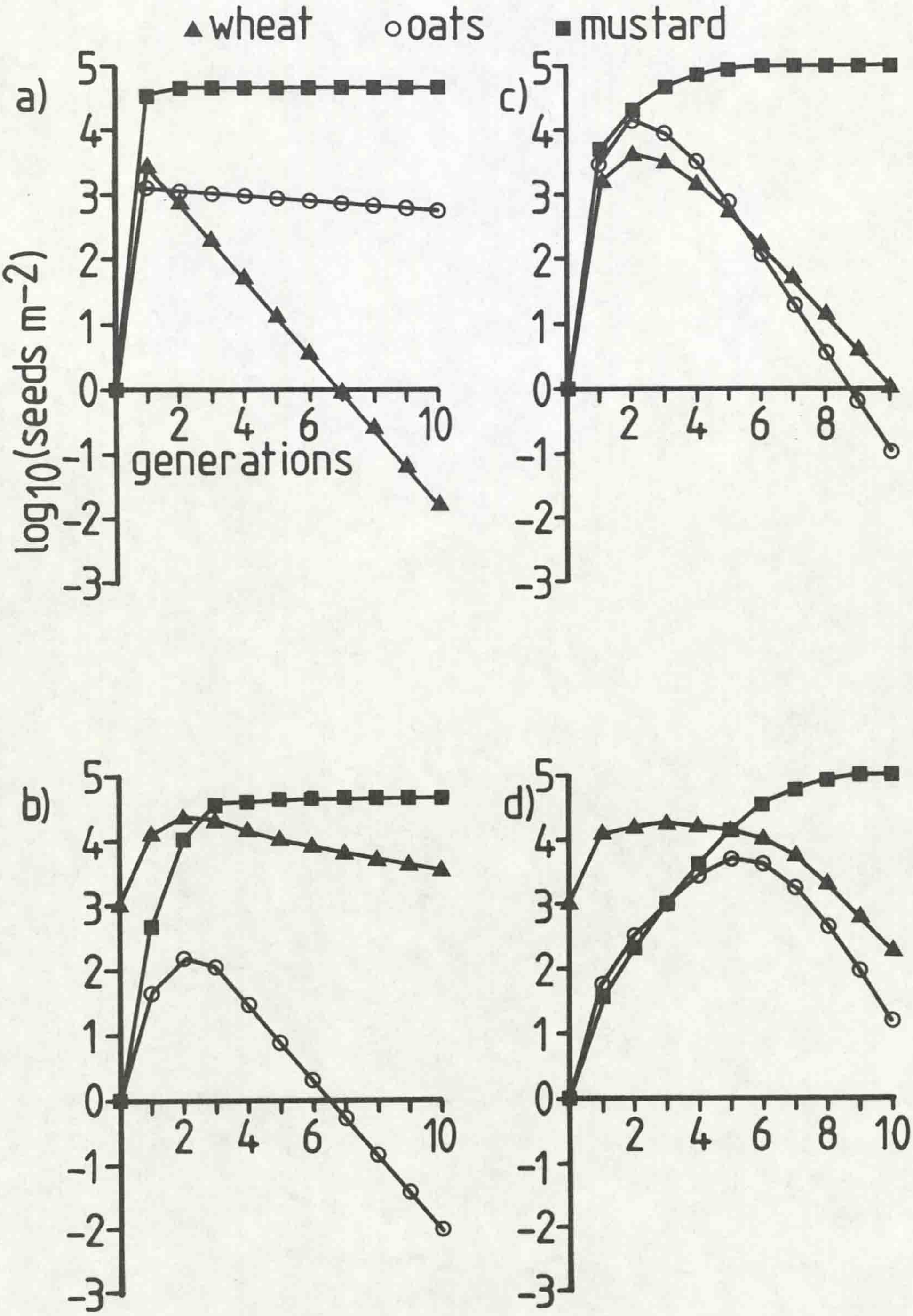
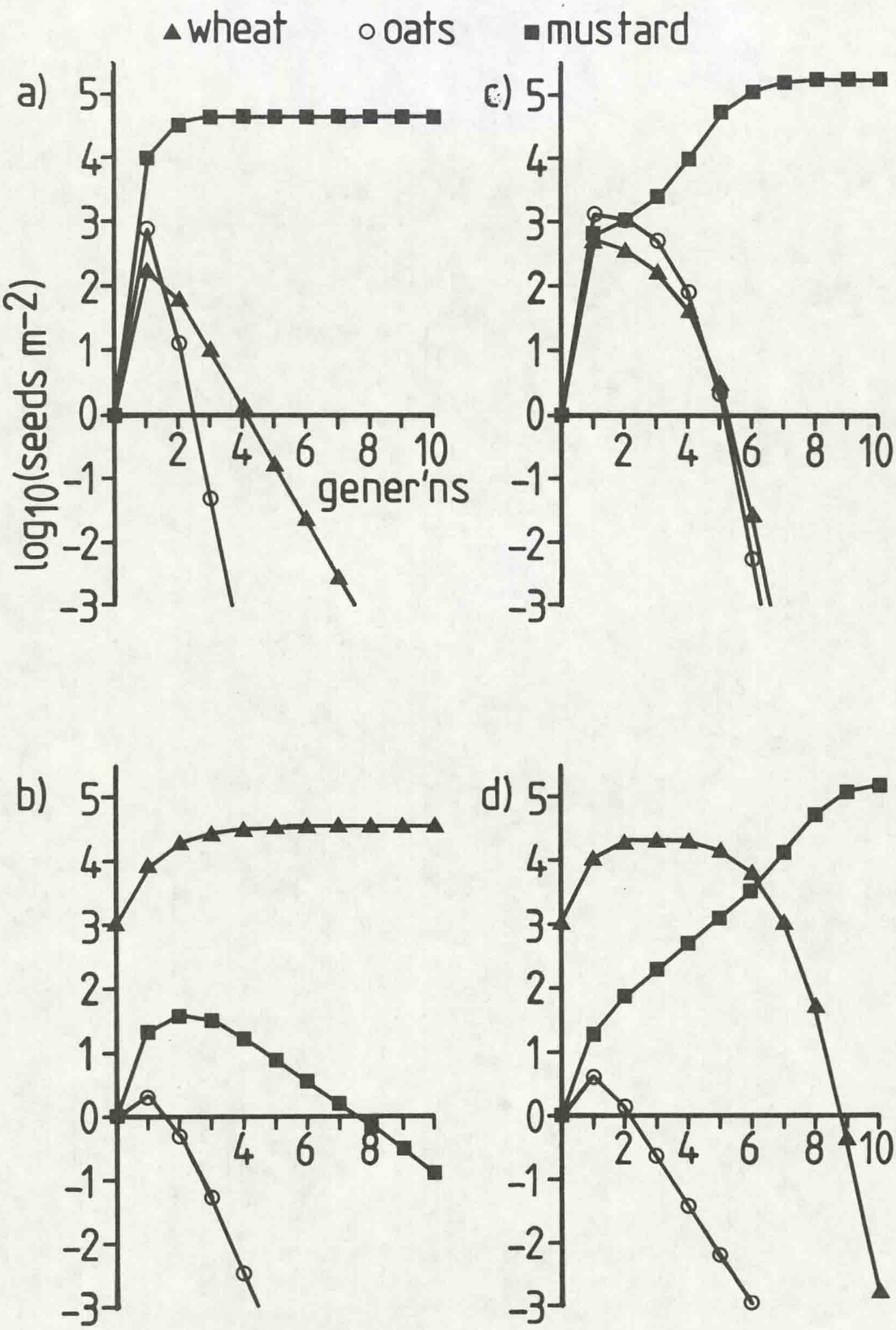


Figure 11. Simulations of community dynamics based on Law and Watkinson models (Table 6). a,b) unsprayed; c,d) sprayed.



mixtures will move towards equilibrium mustard monocultures with 100000 seeds m^{-2}. The Law and Watkinson model again predicts mustard monocultures with 180000 seeds m^{-2} from some initial mixtures, but from others oats will exclude wheat and mustard. If any conclusion can be drawn from these comparisons of models of sprayed and unsprayed mixtures it is that the herbicide appears to be affecting mustard more at low densities and low relative frequencies. The models of sprayed mixtures predict that the mustard displaces the cereals more slowly, even though a higher equilibrium seed density is ultimately reached.This higher equilibrium seed density should not be, perhaps, be trusted, since it represents a significant extrapolation beyond the range of experimental data.

The parameter variation exercise suggests that none of the predictions of these models should be trusted, since parameter variation within 95% confidence limits greatly alters quantitative and qualitative predictions of the models. The equilibrium seed population size in mustard was subject to a 300-fold variation. Moreover, some parameterizations predicted dominance by wheat or oat, and others predicted stable coexistence of wheat and mustard or wheat and oats. Whilst there is no justification for using this level of parameter variation rather than another, the same level of variation in the previous year's experiment changed the predictions of the models very little.

Fitting the model incorporating a control term to the sprayed mustard data did not improve the fit or reduce standard errors of parameters. Table 9 shows the parameter values and standard errors when all parameters were allowed to vary. Estimates of b, α and β remain almost exactly as for the normal Hassell model. Estimates of λ and a (which have a positive correlation of 0.98) have both approximately doubled. The estimate of Λ is very small and positive. A negative value would suggest a biologically implausible negative effect of herbicide on seed yield. However, the standard error is large, and the value is not significantly different from zero (t-

Table 9. Parameter estimates in the Hassell model incorporating control when fitted to data from sprayed mustard.

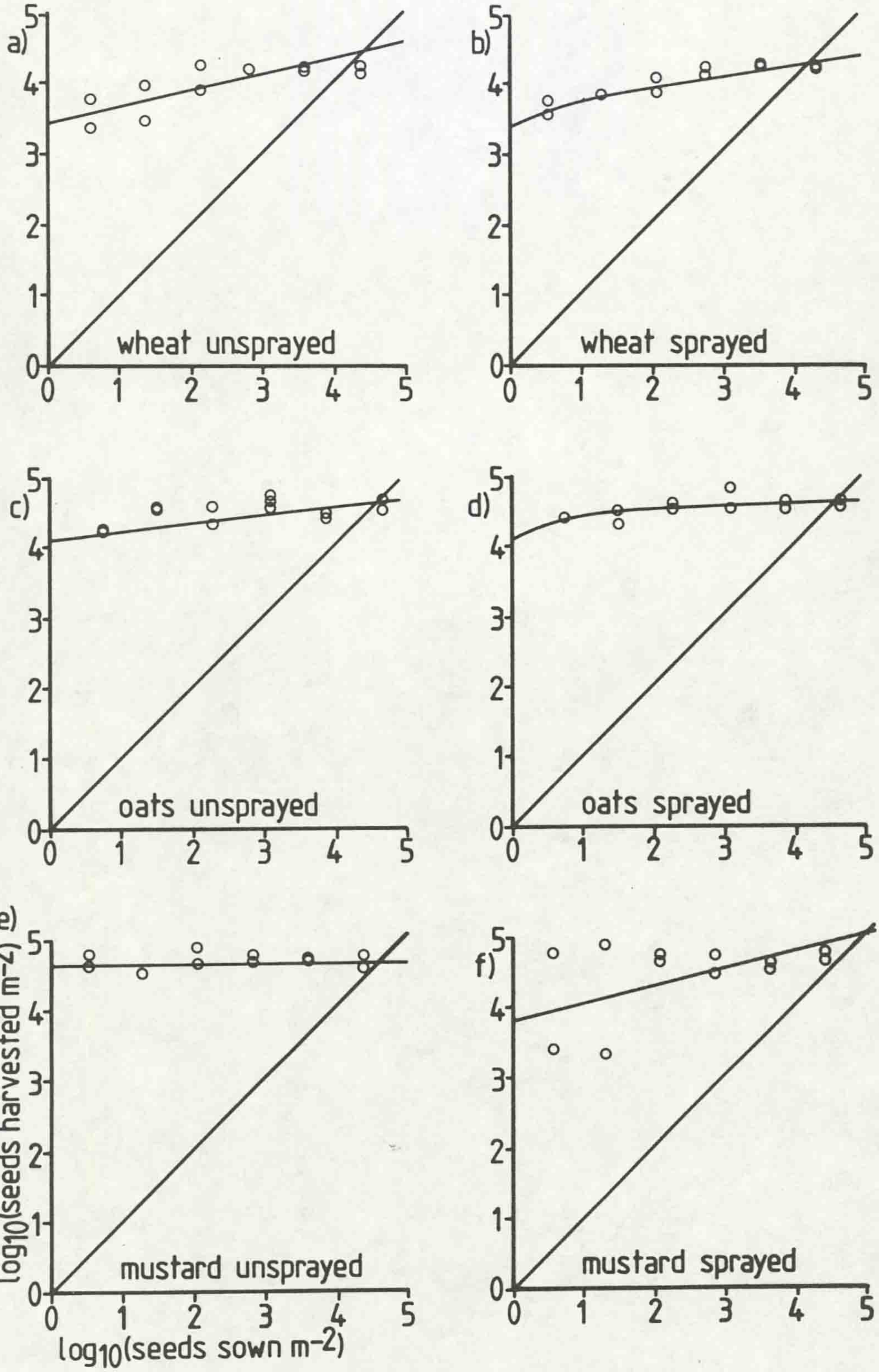
Parameter	Estimate	Standard Error
λ	38.04×10^5	3.17×10^7
a	38.4	19200
b	0.760	0.201
α	0.858	0.641
β	0.832	0.542
Λ	-0.0279	4.80

$R^2 = 0.966$

test, $p>0.05$). This, along with the fact that R^2 is identical to that for the normal Hassell model, suggests that the control term is unnecessary and does not improve the fit. Setting values of λ, b, a, α and β to those of the Hassell models for unsprayed mixtures and allowing only Λ to vary leads to a Λ value of -0.867 (SE 1.20) and an R^2 of 0.945. Again, Λ is not significantly different from zero (t-test, $p>0.05$). Since the data set is the same, the pure error must be the same, and so the lower R^2 means that there is greater lack of fit for the control model.

Examination of graphs of some data and fitted models might provide clues to why models giving robust predictions could not be fitted. Figure 12 shows the monoculture data again, this time with the parts of the Hassell models relevant to monocultures for each species sprayed and unsprayed. Several points are apparent. Firstly, there is very little curvature in the data: all data are from a relatively high density range over which the population yield remains more or less constant and over which individual yields (Figure 8) are density dependent. There is no evidence in the data of the density range over which individual yields would become density independent. Ideally, there should be data from much lower densities, at which the curves might 'tail off' much more. This curvature was rather more apparent in data from the previous year's experiment. Secondly, the lines appear to fit the data poorly. This is because the lines are part of surfaces fitted to data from monocultures, binary mixtures and ternary mixtures together. The implication is that the form of the model does not fit the whole surface well, and data from mixtures are 'forcing' incorrect shapes to the monoculture responses. This problem was also experienced with the Law and Watkinson model. There is, however, no information concerning how well other models might fit. Thirdly, as discussed above, the herbicide treatment appears to have increased variability in the mustard yield data.

Figure 12. Yield / density relationships in monocultures with fitted Hassell models (Table 6). 1:1 lines are shown for reference.



Despite the failure of the models to adequately account for herbicide effects, there is some evidence of an overall depression of mustard yield by 2,4-D. Mustard yield in each sprayed pot was compared with yield in its unsprayed counterpart. In 95 out of 123 comparisons, the yield in the sprayed pot was lower. This ratio of number of pots yielding lower to the number of pots yielding higher on spraying is significantly greater than the 1:1 ratio (χ^2, $p<0.001$). For each comparison, the ratio of yield in the sprayed pot to yield in the unsprayed pot was calculated. The geometric mean of these ratios was 0.55, again suggesting that, overall, mustard yield is lower when sprayed. This figure does not include comparisons in which one pot yielded no seed: in almost all of such cases, however, it was the sprayed pot which yielded nothing, which strengthens the conclusion. It is important to remember that these comparisons are made across wide density and frequency ranges. The effect of herbicide application would not be expected to be uniform across a density range, due to shielding and dilution effects at higher densities.

Discussion.

The mathematical approach to community dynamics used in all these studies failed in this experiment, in that models giving robust, consistent predictions were not obtained. Why should this be, when robust models were generated from the results of a broadly similar experiment the previous year? A major reason appears to be the lack of curvature in at least the monoculture data. Rather more curvature was observed in the previous year's data, even though the lowest density grown that year was slightly higher. An important difference between the two years was the amount of nutrients in the soil, twice as much added fertilizer being present the previous year. The justification for the reduction in nutrients had been that

lower resource levels might intensify competition, supposedly resulting in increased curvature. With hindsight, however, it seems more likely that more intense competition would result in more complete uptake or more efficient use of resources by lower density populations, hence extending the density range over which constant final yield is observed. Other potentially important differences between the experiments include sowing time and differences in weather between years. Any explanation of the lack of curvature can only be speculation without a detailed knowledge of limiting factors on growth of each species, how these limitations change with time, and how they relate to limits on seed yield. This knowledge is entirely lacking.

Another factor which might contribute to the failure of the models in this experiment is that each fit is based on fewer data points than in the previous year. While more pots were used in total, each fit was based on only half of them (sprayed or unsprayed). The number of pots in the experiment was limited by space in the tunnel and time available for harvesting.

A third contributory factor might be an increase in experimental error in the sprayed pots, due to stochastic effects at low densities. However, this could not have had a large effect, since the predictions of the models of unsprayed mixtures were not much more robust than those for sprayed mixtures.

It has not proved possible to draw as many conclusions about the effect of the herbicide as had been hoped. The observations that in 95/123 sprayed/unsprayed pot comparisons the sprayed mustard yielded less seed, and that the geometric mean of all sprayed/unsprayed mustard yield ratios was 0.55, together confirm that the overall effect of the herbicide was to decrease mustard yield, averaged across the density and frequency range. This is more apparent in the mixture data than in the monoculture data shown in Figures 7-9. Similarly, it was tentatively concluded from the comparison of model predictions that mustard yield suffered more at low densities and low relative frequencies. Together, these observations suggest

that the effect of 2,4-D at the dose applied may be to temporarily depress mustard growth: in monoculture, especially at high densities where some individuals may be shielded from herbicide and where a denser canopy may 'dilute' the herbicide from the plants' point of view, the mustard population may recover by later compensatory growth. In mixture, however, the other species continued to grow whilst the mustard was checked, giving mustard less opportunity to capture resources for compensatory growth once it recovered from the check. It must be stressed that this hypothesis can only be very tentative.

This study highlights the dangers of fitting a model and putting faith in its predictions without first searching for its weaknesses. Several studies of this type appear to suffer from this problem. For example, Firbank and Watkinson (1985) fit difference equation models to mortality and fecundity relationships in competing populations of *Agrostemma githago* L. and wheat. Despite the fact that the monoculture data occur over a range in which the model has almost no curvature, the only justification given for the acceptance of these models is the R^2 values. No attempt is made to explore the effect of parameter variation within reasonable limits.

The primary validity of a model is over the range of the data. This does not mean that extrapolation is never permissible, but that it is a very dangerous practice if it is not accompanied by some demonstration of the robustness of the model's predictions.

Chapter 5.

Competition in Mixtures of Annual Weed Species.

"I wende to dede, knight stiff in stowr,
Through fight in field I won the flowr.
No fights me taught the deed to quell-
I wende to dede, sooth I you tell."

Anon.

Introduction.

The plant communities of arable fields have one feature most unusual amongst plant communities. This feature is regular seasonal disturbance of sufficient intensity to almost always preclude survival of the above ground parts of plants. Species generally survive only through underground perennating organs or, more usually, by seed. In most arable weed species, then, plants are destined to die at the end of the cropping cycle. In communities in which plants can perennate above ground, the resources captured and growth made by a plant can either be passed on to its offspring or retained by the plant for the future. This alternative is not open to the annual weeds of agriculture. For them, resources captured must either be passed on to their offspring within the year, or lost when the plant dies. This simple relationship between temporally discrete above ground generations makes such systems more amenable to mathematical modelling than most

other natural communities, since the types of difference equation model discussed in the previous chapters can potentially be applied to them.

The two preceding chapters have considered competitive interactions between annual crop species, firstly under a single management regime and secondly when either treated with a selective herbicide or not. Both studies were carried out with the plants growing in the artificial environment of pots in a polythene tunnel. The situation was also simplified in that the crop species exhibited synchronous germination and all were derived from uniform commercial stocks. The experiment described in this chapter represents the application of the same experimental techniques to a more complex and realistic system. Competition in three binary mixtures of annual weed species in the presence of a crop sown at constant density is studied. The experiment is carried out under field conditions. Some of the weed species have an extended germination period and possess persistent seed banks.

One reason for studying competition in mixtures of crops and weeds is to predict yield loss in the crop (Cousens, 1985). This is of practical importance in planning short term ("tactical") weed control programmes in which control is a response to weed density in the current year (eg Poole and Gill, 1987). Most decisions about weed control are currently based upon these short term considerations. Another approach to weed control is to consider the longer term size of weed populations, "strategic" weed control (Mortimer, 1984, 1987). Decisions about weed control are based on keeping the weed population below a certain density in the long term rather than simply on damage to crop yield in the current year (Cousens *et al.*, 1986; Doyle *et al.*, 1986). Strategic weed control requires an understanding of the population dynamics of the weed and of the influence of control practices on population dynamics. Hence, another practical reason for studying competition in arable

systems is to generate predictive models of weed population and community dynamics.

It is argued in Chapter 1 that designs in which the densities of each species are varied independently are the only type of competition experiment to give results which can be used to predict mixture dynamics. They have been employed in only a few published studies and, apparently, only once under field conditions (Firbank and Watkinson, 1985). They are used in the present study, and mathematical models are fitted to the data in order to predict the dynamics of each binary mixture.

Materials and Methods.

The weed species used in this experiment were *Bromus sterilis* L. (sterile brome), *Avena fatua* L. (wild oat), *Galium aparine* L. (goosegrass or cleavers) and *Sinapis arvensis* L. (charlock). These species were chosen as all being, or having been, serious weeds in Britain, but having diverse growth form and timing of life cycle. *Bromus* is a grass weed, normally lacking a persistent seed bank (Pollard, 1982), with high rates of germination in the late summer and autumn after seed production and dispersal. Its population dynamics have been modelled by Firbank *et al.* (1984, 1985). Seed of *Bromus* used in this study was the progeny of Firbank's populations. *Avena* is another grass weed, but capable of producing a persistent seed bank. Seed may germinate in any of several years after production and burial in the soil: dormancy is affected by both genotype (Naylor and Jana, 1976; Sawhney and Naylor, 1978) and maternal environment (Peters, 1982). Population dynamics of the species have been modelled by Manlove (1985): *Avena* seed used in this study was the progeny of Manlove's populations. *Galium* is a dicotyledonous weed capable of considerable lateral spread by branching and stem growth through a crop canopy, relying

on the crop for support. Germination is highest in autumn, continuing through to spring. It is a relatively recent colonist of arable fields, occurring also in hedges and various other habitats. However, a recent survey of arable weeds in central southern England (Chancellor and Froud-Williams, 1984) showed that it was among the most frequent weed species. Some aspects of the population biology of this species have been studied by Rottele (1980). A number of differences between crop and hedgerow populations of *Galium* have been identified (R. J. Froud-Williams, pers. comm.). The seed used in the present study was taken from hedgerow, rather than crop populations in Knighton-on-Teme, Worcestershire (National Grid reference SO 6270). *Sinapis* is another dicotyledonous weed, with little capacity for lateral spread, but which may exceed the crop in height. Germination occurs in both autumn and spring, but autumn-germinating plants are said to die as a result of severe climate both in Canada (Mulligan and Bailey, 1975) and in England (Edwards, 1980). Very persistent seed banks may be formed. *Sinapis* is sensitive to many selective herbicides and is now less commonly a serious weed. Seed of this species used in this study was obtained from B & S Weed Seeds Ltd: the original source is unknown.

Weeds were grown in a crop of winter wheat, *Triticum aestivum* L. cv Avalon. The experiment was carried out during the 1986-7 season at the University of Liverpool Botanic Gardens, Ness, Cheshire, in a field with a history of arable cropping; an oilseed rape crop had been grown during the previous season, itself preceded by a barley crop.

Three binary mixtures, *Bromus* and *Avena*, *Bromus* and *Galium*, and *Bromus* and *Sinapis* were investigated using designs in which densities of each species were varied independently. The designs were based upon the following densities, chosen after preliminary density trials carried out during

1985-6:

Bromus: 0, 0.845*, 3, 20, 140, 1000 seeds m^{-2}.

Avena: 0, 2.11*, 50, 333, 2330, 16700 seeds m^{-2}.

Galium: 0, 0.920*, 4, 27, 186, 1330 seeds m^{-2}.

Sinapis: 0, 3.15*, 15, 100, 700, 5000 seeds m^{-2}.

* These figures are for plots in which plants were thinned to 1 plant in 2.25 m^2 after germination: they represent the mean sowing density required to achieve this seedling density, based on observed germination rates.

For each pair of species, these basic densities were combined in all possible pairwise combinations to give a wide range of binary mixtures and monocultures. Additional monoculture densities of 2000 seeds m^{-2} for *Bromus* and 2670 seeds m^{-2} for *Galium* were sown. Each treatment was replicated three times. The experiment was laid out in three blocks, each block containing one replicate of each treatment. Positions within each block were randomly assigned.

Wheat was sown using an agricultural seed / fertilizer drill on 28th October 1986 at a rate of 250kg ha^{-1}. A 9:24:24 semi-granular fertilizer was added to the drills at a rate of 375kg ha^{-1}.Weeds were sown into 1.5 x 1.5m (2.25m^2) plots marked by canes on 29th-31st October. Seeds were sprinkled evenly over the surface and incorporated into the soil to a maximum depth of 30mm by raking.

Estimates of winter and spring weed germination were made for each plot over the periods 5th January - 12th February 1987 and 26th March - 15th May 1987, respectively. All other weed species were regularly removed by hand throughout the season. The crop was top dressed with granular ammonium nitrate fertilizer at a rate of 50 kg N ha^{-1} in late March and again in mid-May at a rate of 75 kg N ha^{-1}.

Seeds of each species were harvested by hand in each plot. In each species, seed was shed soon after it ripened. This caused some difficulties

harvesting. At higher densities, seed was estimated on a unit area basis, from either a 0.25m^2 or 1m^2 sub-plot, depending on density. Seed still on plants, seed on the ground (sometimes in a smaller subplot of area 0.04 m^2) and, since they germinated rapidly from the current year's seed production, *Bromus* seedlings, were counted or bagged for later counting. At lower densities, searching the ground for seeds would have proved slow and inefficient: hence, ways of estimating seed which had been shed from plant remains were developed. In *Avena*, glumes persisted on the plant after seed had been shed: a value of 2 seeds per spikelet, the mean of a large number of counts, proved to be a good predictor of seed number. In *Sinapis*, the central septum of each siliqua which had dehisced remained on the plant. Indentations on the septum showed where seeds had been. In *Bromus*, data from a wide range of sizes of intact panicles were analyzed by a linear regression of seed number per panicle against number of primary panicle branches. The equation

$$\text{seeds} = 5.6\ (\text{branches}) - 13.1$$

was obtained. Hence, estimates of total seed for panicles which had shed seed could be obtained from counts of branches. No such methods could be devised for *Galium*, but its large seeds were relatively easily seen on the ground even at quite low densities in large areas. Harvesting began on 10th July 1987 and continued through August, September and October. At the end of October, a few remaining plots (all of them high density mixtures in one block) were abandoned as it had become impossible to obtain reliable seed estimates.

Statistical Analysis.

For each of the three binary mixtures, difference equation models of the relationship between seed sown and seed harvested per unit area were fitted to the data using a least squares non linear regression technique

allowing all parameters to vary together. At the lowest density of each species, where emerging plants were thinned to 1 per plot, germination rates estimated from the lower densities were used to calculate the mean density which would have been sown in order to achieve that seedling density. In the experiments on crops in pots (Chapters 3 and 4) no grounds were found for favouring the Law and Watkinson model over the Hassell model. Hence, only the Hassell model in its two species form was fitted to these data. It is shown in Chapter 2 that it is appropriate to fit the Hassell model without modification to mixtures of weeds in the presence of a crop sown at a constant density. Various transformations of the data were tried in order to choose one which ensured homogeneity of error variance. Log_{10} transformation proved, overall, to give the best distributions. Non linear regression and statistical tests were performed using the SAS package (SAS, 1985).

Goodness of fit was assessed by R^2, adjusted R^2 and two F tests, the first comparing regression mean square and error mean square, the second comparing lack of fit mean square and pure error mean square (Brook and Arnold, 1985). These statistics are discussed more fully in Chapter 3.

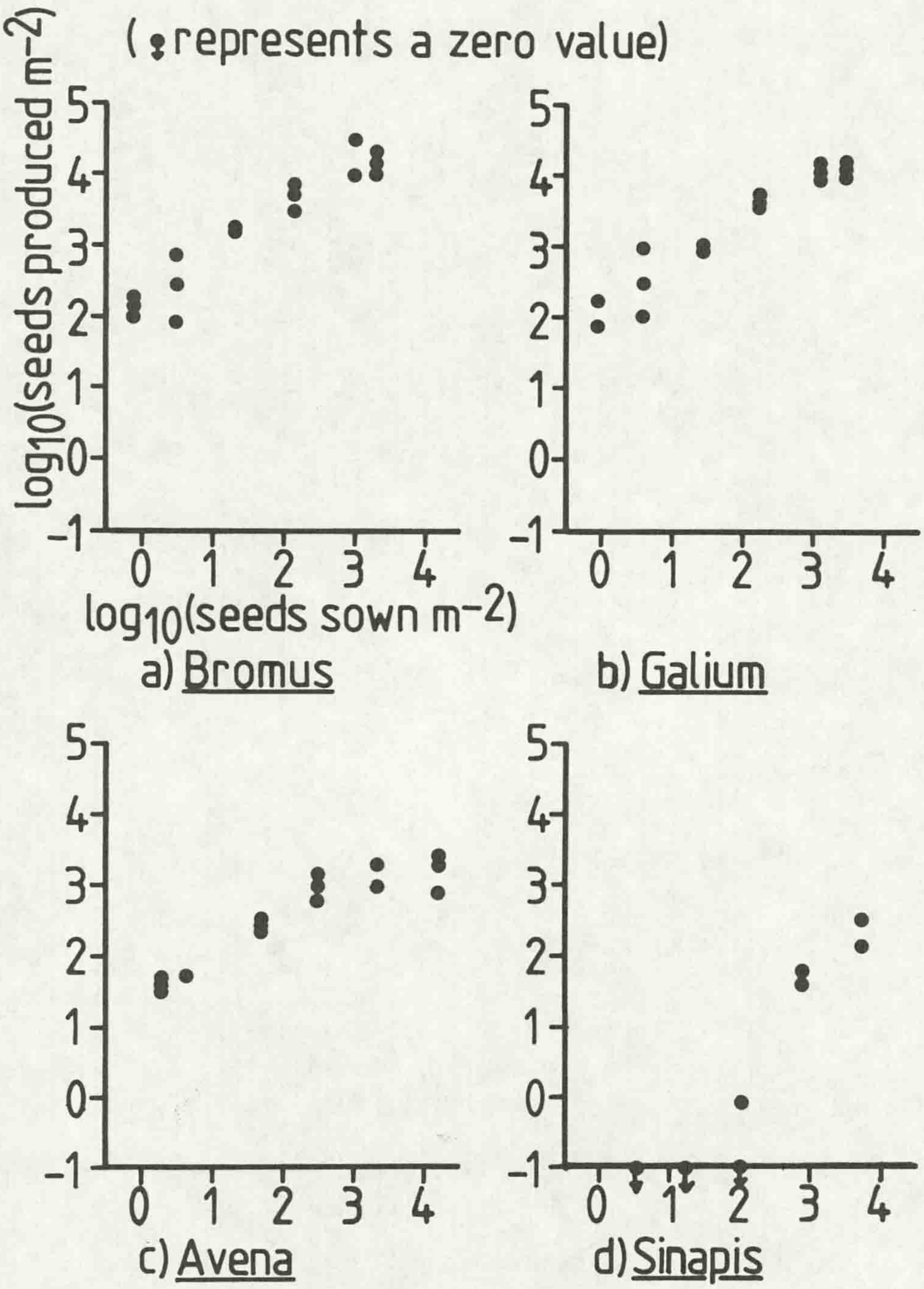
The fitted models relate seed production to seeds present at the beginning of the season. This is not sufficient for prediction of population dynamics, since some of the species have persistent seed banks. The models were extended by incorporating values from the literature for the proportion of seeds remaining alive but dormant over one generation, as in Equation 18 (Chapter 2). The dynamical behaviour of these extended models was then explored by computer simulation. The equations for each species were iterated, taking a wide range of initial binary mixture compositions. Before any faith is placed in these models, it is important to discover how much the conclusions of these simulations depend upon both the estimate of the seed bank survival fraction and the precise parameter values obtained in the

regression. This was investigated by widely varying each parameter value and repeating the simulation for each change in parameterization. The proportion of seeds remaining alive but dormant in the seed bank, S, was first increased to the proportion of seeds remaining ungerminated (i.e. no seed mortality), then decreased to zero (i.e. all ungerminated seeds die). λ and a were together raised to their 95% confidence limits in both species of a mixture together. The value of b was first increased to its upper 95% confidence limit, then decreased to its lower limit. The values of a terms were raised or lowered to 95% confidence limits to favour each species in turn.

Results.

Figure 13 shows seed produced per square metre plotted against seed sown per square metre on $\log_{10}$ axes. As in previous chapters, only data from single species plots are shown for each species. These are not true monocultures since wheat is present at constant density. Graphs for *Bromus* and *Galium* (Figure 13 a, b) show that in these species yield increases with sowing density over the density range sown. Constant final yield is only clearly observed in the higher densities of *Avena* (Figure 13 c). This is in contrast to the results of the experiments with crops grown in pots, in which yield was constant over much of the density range, and did not tail off sharply at the lower densities. This reflects the difficulty of establishing really high densities in field plots, and the lower limit to density in pot systems imposed by pot size. *Sinapis* data (Figure 13 d) show that this species yielded very poorly. In every monoculture plot less seeds were produced than were sown, and in almost every plot less seeds were produced than germinated. All populations were, then, declining. This appeared to be the result of a high mortality rate (>99%) in autumn germinating seedlings. Spring seedlings emerged into a highly competitive established crop and at mortality were small in size and rarely produced many seeds. An analysis of the fecundity

Figure 13. Yield / density relationships in single species plots.



and mortality components of yield / density relationships in these species is not possible since it proved impossible to obtain reliable counts of plant density at harvest.

An understanding of competitive effects in these mixtures requires the analysis of difference equation models fitted to the full range of single weed species and mixture data. Hassell models were fitted as follows for the *Bromus* / *Avena* mixture (from equation 20, Chapter 2):

$$N_{t+1(B)}=\frac{K_{3B}\,N_{t(B)}}{(1+K_{4B}(N_{t(B)}+\alpha_B N_{t(A)}))^{bB}}$$

$$N_{t+1(A)}=\frac{K_{3A}\,N_{t(A)}}{(1+K_{4A}(N_{t(A)}+\alpha_A N_{t(B)}))^{bA}}$$

For the *Bromus* / *Galium* and *Bromus* / *Sinapis* mixtures, similar pairs of models were fitted. The parameters of each of the fitted models, with their standard errors, are shown in Table 10. The fitting routine failed to converge for the model of *Sinapis* in the presence of *Bromus*. This is probably a result of the high degree of variability in the data set, and the large number of zero values (converted to a nominal 1 seed m^{-2} before $\log_{10}$ transformation). In the remaining models, which were successfully fitted, the values of K_3 are strikingly lower than the values of λ obtained for crops in pots. λ represents the maximum attainable yield of isolated plants whilst K_3 represents the maximum yield of an isolated plant in a constant density of crop. This difference in size of values almost certainly represents the competitive effect of the crop rather than any intrinsically lower capacity for seed production in the weeds. The definition of the parameter b in the Hassell models is unchanged by the presence of a constant density of crop. This is because it relates to the way in which the species compensates for changes in its own density at high densities, since these models of mixtures are based on the assumption that individual of one species are proportional in their effect on another species to individuals of that species. These values are all less than

Table 10. Parameter estimates and (in brackets) their asymptotic standard errors in best-fit Hassell models.

	Bromus / Avena		Bromus / Galium		Bromus / Sinapis	
Parameter	Bromus	Avena	Bromus	Galium	Bromus	Sinapis
K_3	97.6 (20.1)	16.0 (5.96)	117 (17.3)	163 (371)	146 (18.1)	*
K_4	0.0227 (0.0283)	0.0702 (0.0634)	0.0265 (0.0278)	1.50 (10.3)	0.0546 (0.0379)	*
b	0.727 (0.266)	0.705 (0.0713)	0.713 (0.162)	0.397 (0.0881)	0.654 (0.107)	*
α	0.00132 (0.00257)	1.27 (0.631)	-0.00628 (0.0124)	4.14 (3.99)	0.00258 (0.00273)	*

* Non-linear regression routine did not converge.

Table 11. Goodness of fit of the models.

R^2 is the coefficient of determination.

adj R^2 is the adjusted coefficient of determination.

F_1 is the F value for the comparison of regression / total error, where rejection of the null hypothesis as fitting well.

MS(LF) is the lack of fit mean square.

F_2 is the F value for the lack of fit / pure error comparison, where rejection of the null hypothesis leads to rejection of the model as giving optimal fit to the data.

	Bromus / Avena		Bromus / Galium		Bromus / Sinapis	
	Bromus	Avena	Bromus	Galium	Bromus	Sinapis
R^2	0.984	0.982	0.992	0.968	0.995	-
adj R^2	0.983	0.981	0.991	0.965	0.995	-
F_1	977 ***	837 ***	1850 ***	456 ***	3000 ***	-
MS(LF)	0.216	0.168	0.117	0.512	0.0523	-
F_2	1.62 NS	1.81 *	1.72 *	3.99 ***	1.01 NS	-

Significance levels for F-tests:

*** rejection of null hypothesis at 99.9% level.

** rejection of null hypothesis at 99% level.

* rejection of null hypothesis at 95% level.

NS acceptance of null hypothesis at 95% level.

unity, lying between 0.39 and 0.73. If these values are to be believed, the implication is that *Bromus*, *Galium* and *Avena* under-compensate in yield for changes in density at high densities. On the other hand, it is possible to argue that these low values are the result of fitting models to an imperfect range of data which inevitably contain experimental error. The data from *Bromus* and *Galium* do not include the really high density plots from which the best estimates of b would be obtained. This, combined with experimental error, leads to correlated parameter estimates which, whilst together giving a model which describes the data well, cannot necessarily be trusted individually. These two possibilities cannot easily be distinguished in *Bromus* and *Galium*, but in *Avena* there is some tailing-off in high-density data, suggesting that poor estimation of b is less likely to be a problem. Values of α in the Hassell model are equivalence coefficients representing the number of plants of a second species which have the same effect on the yield of a first species as one individual of the first species (see Chapter 2). The *a* values for *Bromus* in the presence of each of the other species are very close to zero, suggesting that it is affected very little by them. This could be the result of either niche separation or superior competitive ability. The negative value of α for *Bromus* in the presence of *Galium* might appear to suggest that the presence of *Galium* tends to increase the yield of *Bromus*. However, the value is very close to zero, and smaller than its standard error, so no biological meaning should be attached to the negative sign. The values of α for both *Avena* and *Galium* are greater than 1. The presence of individuals of *Bromus*, then, depress their yield more than the presence of the same number of individuals of their own species. This result favours the suggestion that the relative success of *Bromus* in mixture is a result of superior competitive ability rather than niche separation.

Table 11 shows goodness of fit statistics for each model. R^2 and adjusted R^2 values all exceed 0.96, indicating that a very large proportion of the

variation in this data is explained by the model. The first F test, comparing regression mean square and total error mean square confirms this: in all cases the null hypotheses are rejected at the 99.9% level. However, the second F test shows that for only two models, those of *Bromus* in the presence of *Avena* and *Bromus* in the presence of *Sinapis*, was there no significant lack of fit, and in one model (*Galium* in the presence of *Bromus*) lack of fit was very highly significant ($p<0.001$). These F values depend, however, upon the background of pure error against which lack of fit is observed (see Chapter 3). Lack of fit mean square provides an absolute measure of lack of fit: comparison of this statistic with the F values shows that one of the two models with no significant lack of fit had, in fact, the second highest lack of fit mean square. Only the model for *Galium* stands out as having a high lack of fit mean square, as well as a highly significant lack of fit and comparatively large standard errors of parameters (Table 10). There might here be some case for fitting an alternative model. Law and Watkinson (1987) advocate the use of the model referred to colloquially in this thesis as the "Law and Watkinson model" (equation 13, Chapter 2) on the grounds of its generality of form and its giving less lack of fit than the Hassell model when fitted to one data set. This model was fitted to the *Galium* data in the hope of obtaining a better fit. Lack of fit mean square was only marginally reduced, however, and the significance level in the second F test was not changed. Whilst not being optimal, the Hassell models in general appear to give an adequate fit, and were used in the simulation exercises.

The Hassell models described so far relate seed production to seed sown. Since some of these species form persistent seed banks, these models are insufficient to predict population and community dynamics. The models must be extended as in equation 18 (Chapter 2) by incorporating the value of S, the proportion of seeds remaining alive but dormant in the seed bank over one generation. The assumption is made that each dormant seed surviving

to the beginning of a generation has the same probability of germination, however many years the seed has been dormant. This may not always be true, at least in *Avena fatua* (Wilson, 1985). There is no evidence of persistent seed banks in *Bromus sterilis* from this or other studies (Firbank , 1984), so *Bromus* models did not need to be extended. Whilst there is evidence for persistent seed banks in *Sinapis* (Mulligan and Bailey, 1975; Edwards, 1980), it was not possible to fit a Hassell model to *Sinapis* data. However, since even at low densities fewer seeds were produced than germinated, any extrapolation from this season's behaviour must predict decline of the population to extinction, whatever the seed bank dynamics. Wilson (1985) gives values for *Avena fatua* seed survival in the soil in winter barley crops, for three years' seed crops, each followed for four years. The mean proportion of seeds surviving dormant over one year with yearly ploughing was 0.39. This S value was tentatively incorporated into the *Avena* model. Rottele (1980) gives S values for *Galium aparine* grown in a wide range of crops in West Germany. These cannot be used directly, however, since his populations exhibited a much lower germination rate than was observed in the present study. It can be calculated that the mean survivorship of ungerminated *Galium* seeds in a winter wheat crop over a single season was 0.9. Taking a germination rate of 0.5 from the present study, estimated from lower density plots, an S value of 0.45 is obtained. This was incorporated into the *Galium* model.

Figures 14 and 15 show some examples of simulations of community dynamics in the *Bromus / Avena* and *Bromus / Galium* mixtures, obtained by iteration of the models extended to include seed bank survivorship. In each figure, a) - c) show simulations of trajectories from three different initial community compositions. The assumption is made that seed losses between dispersal and germination of the first cohort of seedlings are negligible. The models for *Bromus* and *Avena* predict that *Bromus* drives *Avena* quite

Figure 14. Simulations of dynamics of *Bromus* / *Avena* mixtures, based on the Hassell models (Table 10).

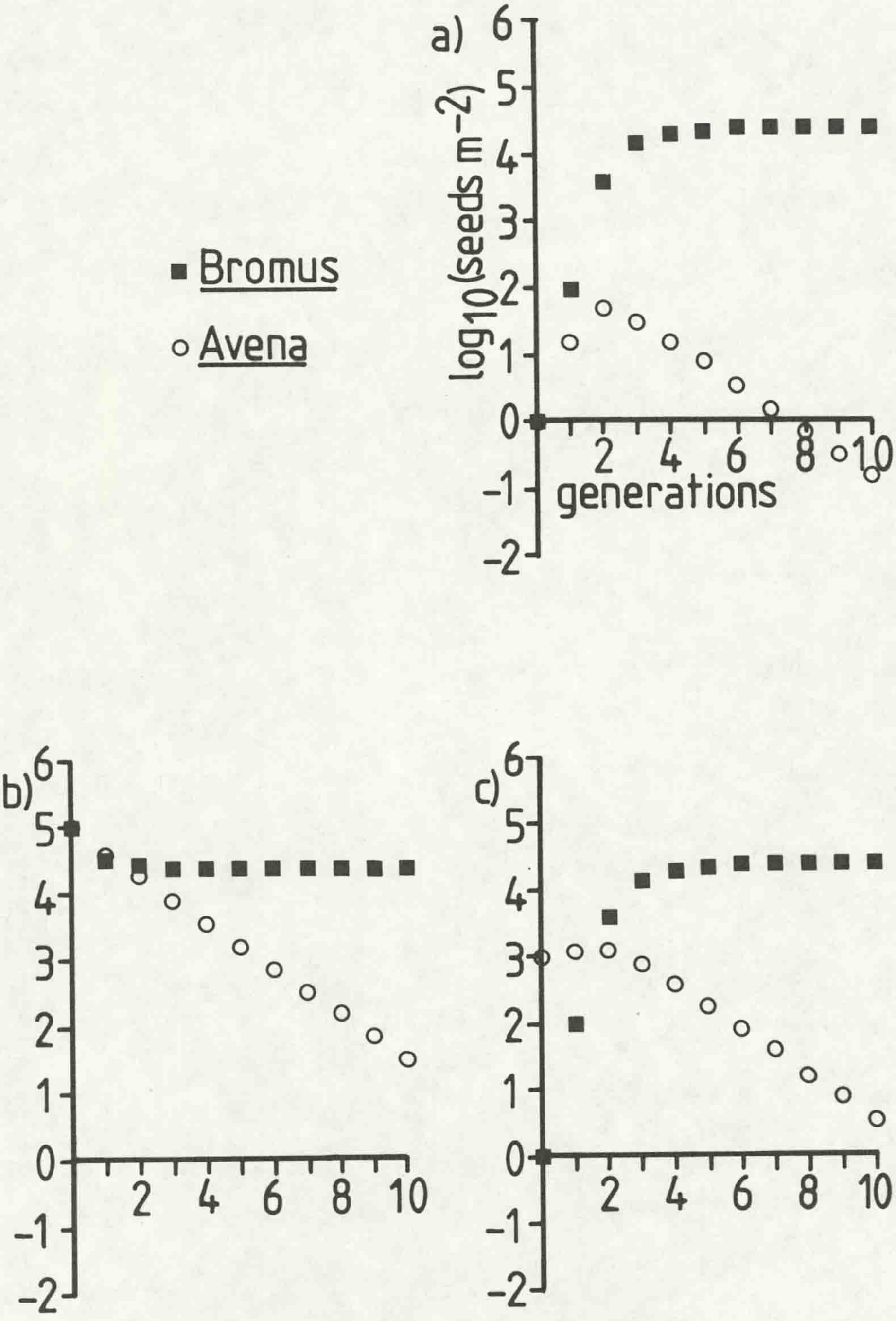
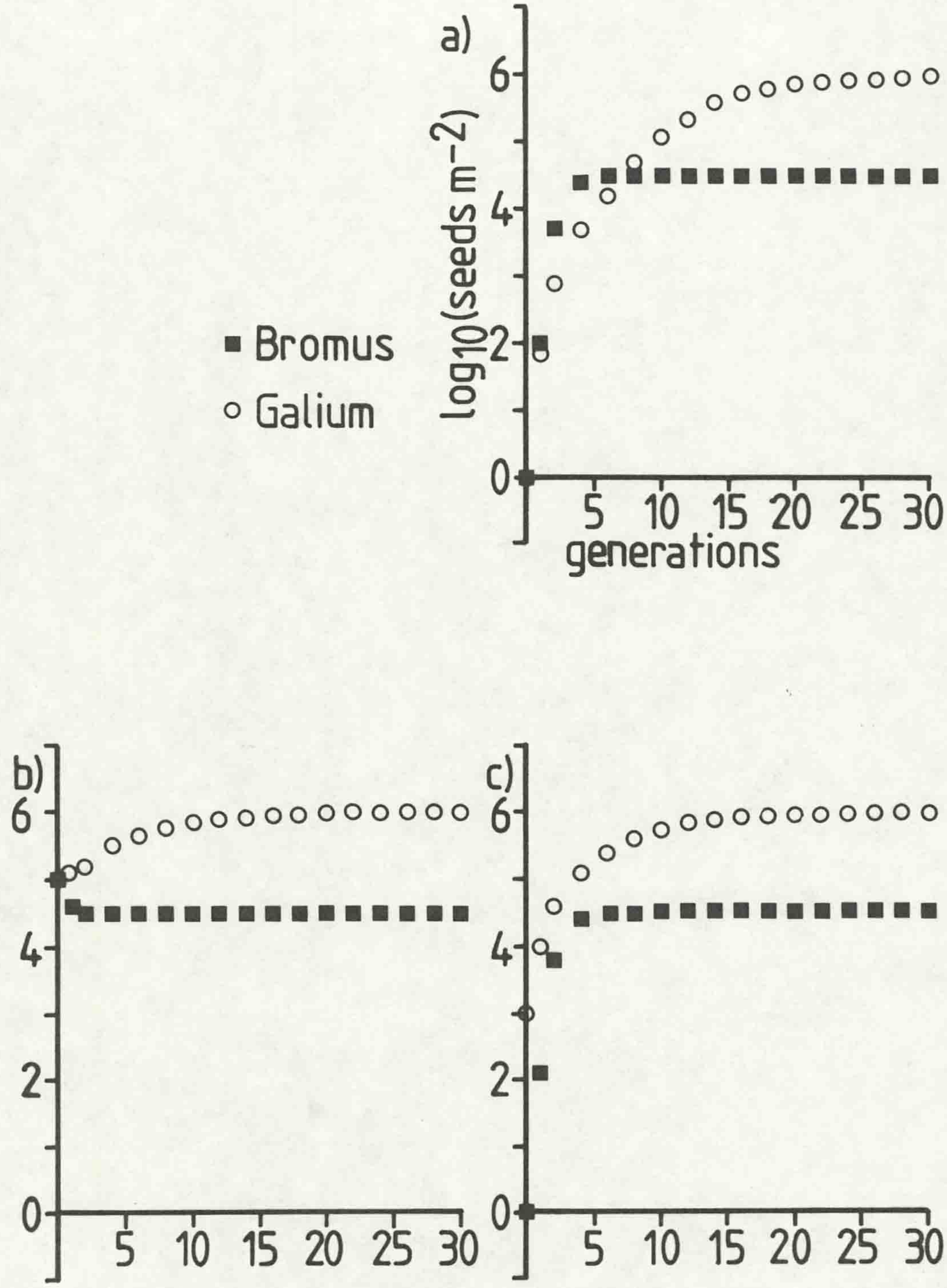


Figure 15. Simulations of dynamics of *Bromus* / *Galium* mixtures, based on the Hassell models (Table 10).



rapidly towards extinction, *Bromus* monotonically approaching an equilibrium density of 24000 seeds m^{-2}. This conclusion appears to hold irrespective of starting densities. The models for *Bromus* and *Galium*, however, predict that mixtures move from any starting densities towards a stable equilibrium, with 36000 *Bromus* seeds m^{-2} and 970000 *Galium* seeds m^{-2} in the seed bank at the start of a generation. The model for *Bromus* in the presence of *Sinapis*, along with the conclusion reached above that *Sinapis* populations will decline to extinction, suggests that equilibrium *Bromus* density would be 37000 seeds m^{-2}. The interpretation of these data by fitting difference equation models depends upon the least squares regression technique and on the approximate values of S for *Avena* and *Galium*. Whilst these models give the best fit, it is possible that others, fitting almost as well, might seriously alter the predictions of the models. The similarity in predictions of equilibrium *Bromus* density suggests that at least some confidence may be placed in these models. The parameter variation exercise, however, provides a greater challenge to the robustness of these models. In the *Bromus / Avena* mixture, only one of seven reparameterizations affected the qualitative conclusion. This was the manipulation of α values intended to favour *Avena* most: the models then predicted a stable equilibrium dominated by *Bromus*. In all the other reparameterizations, the conclusion that *Bromus* drives *Avena* to extinction was unchanged, although the predicted equilibrium density varied widely. In the *Bromus / Galium* mixture, some reparameterizations predicted slow replacement of *Galium* by *Bromus*, whilst others predicted chaotic behaviour. Some did not alter the qualitative predictions. In neither mixture did variation of S affect the qualitative predictions. It appears, then, that some confidence may be placed in the predictions that *Bromus* will drive *Sinapis* and *Avena* to extinction. The balance between *Bromus* and *Galium* appears to be a fine one.

Discussion.

The results of this study demonstrate that difference equation models of population change can be applied not only to carefully controlled systems of plants growing in pots, but also to more complex and realistic field systems. In all cases except that of *Sinapis*, it was possible to fit models by regression: the inability to fit models to *Sinapis* data is a result of its failure as a weed of a winter crop, rather than greater experimental error due to field conditions themselves. The theoretical prediction (Chapter 2) that it should be possible to fit Hassell models which do not include explicit crop density or crop growth parameters to data from mixtures of weeds in a crop sown at a constant density is also confirmed. Ideally, however, the theoretical analysis would need to be confirmed by repeating the experiment in the presence and absence of the crop. This would allow verification that the term b was unchanged by the presence of the crop and that the derived parameters K_3 and K_4 were formulated correctly.

In some respects, planning of experimental protocol in the field system was easier, since fewer arbitrary decisions about growth conditions and timing needed to be made than in the pot system. Time of sowing and timing and rates of fertilizer application were determined by normal agricultural practice and weather conditions. No decision needed to be made about when to cease watering. Ideally, harvesting of all plots should have been simultaneous at a time determined by the ripeness of the crop. This was impractical, but this did not affect the seed yields of the weeds since all seed had been set by the time the crop was ripe.

A major difference between mixture experiments carried out in pots and in the field is the density range which can be achieved. Pots set a rather high lower limit to the density range, but allow very high densities to be established easily. In the field, low densities can easily be established but very high densities would require prohibitive amounts of seed. Such high

sowing densities could also lead to density dependent predation or disease which would be harder to prevent or control in the field than in pots under cover. Whilst density dependent predation and disease are probably important factors in the regulation of some natural populations, it is not clear whether their effects could be modelled by these functions, and it is preferable that they should be excluded from an exploratory study such as this, rather than be allowed to intervene in an arbitrary and uncontrolled fashion. The possible criticism that very high densities should not be included if they exceed densities observed in the field is, however, invalid. Data concerning what would happen to a population if it did occur at those densities should help, rather than hinder, the understanding and prediction of what happens at the densities at which it does occur.

The predictions of community dynamics made using these models are based not only upon the assumption that the relationship between yield and density can be extrapolated beyond the range of the data, but also on the assumption that this relationship remains the same each year: neither assumption may be true. Whilst the environment of plants grown under cover can be controlled to some extent, populations grown in the field are exposed to the full force of climatic variation. On the assumption that models whose predictions are robust when exposed to arbitrary parameter variation will also be robust in the face of seasonal variation, the parameter variation exercise can give some idea of how much confidence can be placed in the predictions of the models. On these grounds, the conclusion that *Bromus* will drive *Avena* and *Sinapis* to extinction appears robust. The balance between *Bromus* and *Galium* appears to be much finer, however, and whilst the species may persist together, no confidence can be placed in the prediction of a stable equilibrium. The most critical test of the models must be to take the seeds produced in a number of plots and sow them in winter wheat at the beginning of the next season. The predicted yields could then be compared

with those observed. It did not prove possible to carry out this test, although the experiment described in Chapter 6 acts as a partial test.

Variations in husbandry practice and weed control are also likely to affect the predictions of the model. If difference equation models of weed population and community dynamics are to be of practical value in forecasting weed infestations and in making herbicide recommendations, knowledge of how the effects of these practices can be incorporated into the models in terms of both structure of the models and parameter values is essential. This has yet to be tackled directly, but Chapter 6 describes an investigation into the degree to which a range of husbandry practices alter community trajectories in mixtures of the four species used in this experiment over several generations.

Whilst most husbandry practices are seen as modifiers of competitive interactions, the annual disturbance associated with harvesting the old crop and sowing the new has a more basic role. It is this disturbance which prevents perennation of the above ground parts of plants, necessitating any resources which are to be passed on to the next generation to be concentrated in a propagule bank. This restricts community change to small scale dynamical rather than larger scale successional change. It is also this which allows this simple modelling approach to have any biological relevance or predictive success.

Chapter 6.

The Dynamics of an Annual Weed Community.

"Against the rubber tongues of cows and the hoeing hands of men
Thistles spike the summer air
Or crackle open under a blue-black pressure.

. . .

Then they grow grey, like men.
Mown down, it is a feud. Their sons appear,
Stiff with weapons, fighting back over the same ground."

Ted Hughes.

Introduction.

Agricultural plant communities, both arable and grassland systems, represent arrested secondary successions. Severe annual disturbance and heavy grazing, respectively, prevent large scale and long term successional change in community structure. These communities, however, may still change on a smaller scale (community dynamics), in terms of both species composition and relative abundance of species. A few long term studies of grassland communities illustrate the extent of community change. In a study over 12 years of (mainly rare) herbaceous perennial species in a grassland community in Upper Teesdale, Bradshaw (1981) showed that whilst there was variation in population sizes between years, many populations fluctuated between quite narrow limits. An even longer term study on an enclosed plot of grassland in the Breckland (Watt, 1981; Davy and Jefferies,

1981) gave different results. Over a period of 44 years, *Festuca ovina*, *Hieracium pilosella* and *Thymus* species displayed successive periods of dominance, each lasting between 10 and 20 years, before declining to low levels. Watt (1981) interpreted these changes in terms of competition, climatic change and the declining vigour of even-aged stands. Viewed on a shorter time scale, however, the community might appear to be rather stable. For example, in the same type of community it was found that over a 4 year period the population of *Hieracium pilosella* rosettes remained remarkably constant in size despite an annual turnover of about 25% of rosettes (Bishop *et al.*, 1978). The concept of stability must, then, be related to the time scale and spatial scale on which it is observed. Cyclic changes in community structure (Watt, 1947) and invasion of species from other communities may act on longer time scales than those of most experimental studies.

The experiments described in Chapters 3, 4 and 5 investigate the outcome of competition in mixtures of crop or weed species over a single year. Typically such experiments relate seed sown to biomass or seed harvested and models may be generalised to describe changes over generations, by including terms describing post dispersal loss prior to germination and the fraction of seed persisting in the persistent seed bank. Mathematical models were fitted to the data, which were then used to make predictions of community dynamics over several years. Scientifically it is necessary to validate this approach by an experimental study of community dynamics over several years in a system about which predictions based on a single year's yields have been made.

Experimental studies of arable community dynamics are rare in the literature. A number of purely descriptive weed surveys of various areas have been made (eg. Chancellor and Froud-Williams, 1984; Mutkula *et al.*, 1969; Roberts and Stokes, 1966). Chancellor (1985) describes in detail the changes in the weed community of a single arable field over the 20 years

following ploughing of pre-existing grassland, during which time several crops were grown and various husbandry practices were used. The number of species varied widely between years, as did seedling density. The transition from arable weed to grassland weed floras is well documented, but even such a detailed descriptive study cannot take the place of experimental studies in elucidating the dynamics of the arable community: possible causes of changes can be suggested but not tested. In a rare experimental study, Mahn and Helmecke (1979) investigated effects over 5 years of several herbicides at different dose rates on species composition and dominance structure of the weed communities of experimental plots within a cereal field. Herbicide application changed the number of individuals and the dominance structure in various ways, with almost no change in the species present in the community. Similar conclusions can be drawn from the results of a much longer study of the effects of annual application of the herbicide 2,4-dichlorophenoxyacetic acid (2,4-D) on the weed community in a wheat crop (Hume, 1987). No weed species were eliminated over the 36 years of the experiment, and no new species became established as a major constituent of the community as a result of herbicide application (those species which did become established also became established in unsprayed control plots). The only changes in community structure resulting from herbicide application were quantitative changes in the relative abundance of species.

This chapter describes an experimental study of the dynamics of a community consisting of the 4 weed species investigated in Chapter 5, in a winter wheat crop, over $2^1/_2$ years. It provides a partial test of the predictions made in Chapter 5 on the basis of a single year's results. Replicate communities were established under a range of husbandry practices in order to indicate the magnitude of the effects of management regimes, which must

ultimately be incorporated into the models of weed community dynamics if they are to be of practical value.

Materials and Methods.

The experimental weed community consisted of *Bromus sterilis* L. (sterile brome), *Avena fatua* L. (wild oats), *Galium aparine* L. (goosegrass, cleavers) and *Sinapis arvensis* L. (charlock) in the presence of winter wheat, *Triticum aestivum* L. cv. Avalon. These species were chosen as being, or having been serious annual weeds in Britain, with diverse growth form and timing of the life cycle: their characteristics are described more fully in Chapter 5. The experiment was carried out in a field with a history of arable cropping (winter wheat in the previous two seasons) at the University of Liverpool Botanic Gardens, Ness, Cheshire.

The experiment was based on a factorial design. One factor, density, related to the initial density at which the community was established. The others (cultivation and herbicide) were as follows (the term "seed" is used loosely so as to include the single seeded fruits of *Galium* and the caryopses of the grasses):

Density: **i)** "High": sowing densities (seed m^{-2}) of 1000 *Bromus*, 600 *Avena*, 600 *Galium* and 4000 *Sinapis*.

ii) "Low": sowing densities (seed m^{-2}) of 5 (thinned on emergence to 3) *Bromus*, 50 *Avena*, 50 *Galium* and 100 *Sinapis*.

Cultivation: **i)**: "Unploughed": harvest followed by paraquat application and disc harrowing to a depth of 30mm.

ii): "Ploughed": harvest followed by paraquat application, ploughing (soil inversion to a depth of 200 mm) and disc harrowing.

Herbicide: **i)**: "Unsprayed": no herbicide applied.

ii): "Wild oat herbicide": treated with the herbicide Commando (active ingredient 20% w/v L-flamprop-isopropyl) at a rate of 3 l ha^{-1} in 400 l water ha^{-1} at the 3 node growth stage of wheat (stage 33, Zadoks *et al.*, 1974), in late May.

iii): "Wild oat and broadleaf herbicides": treated with the herbicide Broxolon (active ingredients 20 g l^{-1} dichloropicolinic acid, 96 g l^{-1} bromoxynil as octanoate, and 456 g l^{-1} mecoprop as its butoxy ethyl ester) at a rate of 3.5 l ha^{-1} in 300 l water ha^{-1} during April, followed by the herbicide Commando as above.

Each combination in the factorial design was replicated three times, replicates being assigned to separate blocks. Each block was split according to cultivation, to ease tractor work. Plot positions within each half block were assigned randomly.

The experiment was set up in autumn 1985 on a site which had been prepared by treatment with glyphosate to kill weeds, followed 3 weeks later by disc harrowing. Wheat was sown at a rate of 250 kg ha^{-1}, and a 9:24:24 semi-granular fertilizer was added to the drills at a rate of 375 kg ha^{-1}, using an agricultural seed / fertilizer drill. Weed seeds from the stocks described in Chapter 5 were sprinkled onto the surface of 2m x 2m plots on 29th - 31st October, and incorporated into the top 30mm of the soil by raking. Estimates of seedling densities of each species in each plot were made during the period 13th - 19th March 1986 by sampling 0.25 m^2 sub-plots in low density plots and 0.09m^2 sub-plots in high density plots. All other weed species were regularly removed by hand throughout the season: this required, in total, approximately 150 man-hours. The crop was top-dressed with a granular ammonium nitrate fertilizer at a rate of 50 kg N ha^{-1} in late March and again at a rate of 75 kg N ha^{-1} in mid-May. Herbicide applications were made to the appropriate plots as described above. Seeds of each species

were harvested by hand in each plot. Seed still on plants, seeds on the ground, and *Bromus* seedlings (all from the current year's seed production) were collected from a 0.25 m^2 sub-plot located near the centre of the main plot, counted, and returned to the plot. *Avena* seed production was estimated from the whole plot. Wheat and weeds were then cut in each plot in turn, using a reciprocating mower and leaving a stubble 50 - 100 mm in height. Wheat and as much of the vegetative parts of weeds as possible were removed, weed seeds being left in the plots. Germinating seedlings were killed by paraquat before the seed bed was prepared for the next year's crop, either with or without ploughing. Seed produced in 1986 was allowed to germinate in the plots during 1986-7. The plots were managed and harvested as before, counts of seedlings being made during the period 26th - 30th March 1987 by sampling 0.25 m^2 sub-plots in ploughed plots and 0.09m^2 subplots in the denser unploughed plots. Larger sub-plots of 1 m^2 were harvested in 1987. The procedure was repeated for the 1987-8 season, but the plots were abandoned after seedling counts had been made on 28th and 29th March, 1988.

In addition to these plots sown in 1985, four further plots of the same size were established in 1986 on the same site. Seeds were sown at the same rates as in 1985, two replicate plots at low density and two at high density. These plots were treated in the same way as the other unsprayed plots during 1986-7.

Results.

Results are presented in two ways. The first is the graphical representation of community trajectories under each combination of husbandry practices and initial community compositions. The second is the identification of factors whose different treatments give rise to significant differences in the success

of a species, by analysis of variance of yield or seedling density data for each species at each census point.

Community trajectories can be based upon two separate facets of community composition, number of seedlings present in March, or number of seeds present at harvest. The duration of the experiment allows 3 points to be taken for each trajectory, March seedling counts in 1986, 1987 and 1988, and seed counts at sowing in 1985, harvest in 1986 and harvest in 1987. The seed densities sown are assumed to be approximately equivalent to seed densities at a hypothetical 1985 harvest. March seedling data may be used as collected, but harvest data must be augmented by estimates of the numbers of seeds surviving in the seed bank. Soil cores were taken from a number of plots prior to seed being shed in 1987 in order to estimate the size of the buried seed bank. Unfortunately, the cores proved too small to give reliable estimates, due to miscalculation of the soil volume required to yield an adequate number of seeds. Hence, values derived from the literature for the proportion of seeds remaining alive but dormant over one generation of 0 for *Bromus*, 0.39 for *Avena* and 0.45 for *Galium* were used, as discussed in Chapter 5. No seed production by *Sinapis* was observed in these plots in either 1986 or 1987: the seed population clearly must have been declining, so for simplicity *Sinapis* has been omitted from the trajectory diagrams.

Mean trajectories of communities are shown in Figure 16 for harvest data and Figure 17 for seedling counts. In no cases were standard errors greater than 6% of mean values, and no confidence limits nor standard error bars are shown to maximise clarity. Analyses of variance (Table 13, see below) provided a rigorous statistical treatment of the data.

Figures 16 a) and b) show community trajectories in terms of seeds at harvest for ploughed, unsprayed plots starting from high and low densities respectively. The results of the competition experiments on binary mixtures of weeds described in Chapter 5 relate most closely to these data. In all cases

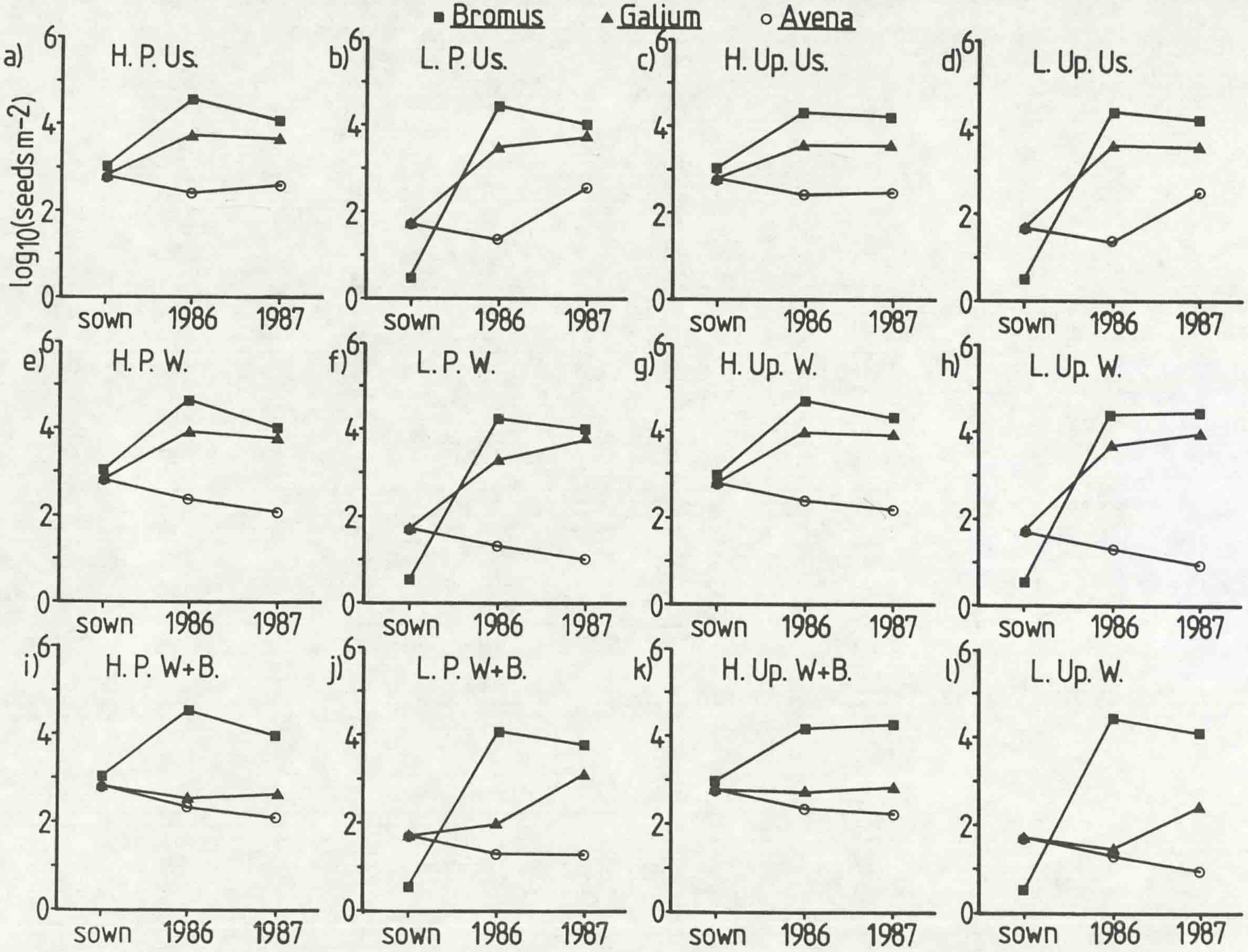


Figure 16. Trajectories based on seed densities.
Treatments: Density: H High, L Low.
Cultivation: P Ploughed, Up Unploughed.
Herbicide: Us Unsprayed, W Wild oat herbicide, W+B Wild oat and broadleaf herbicides.

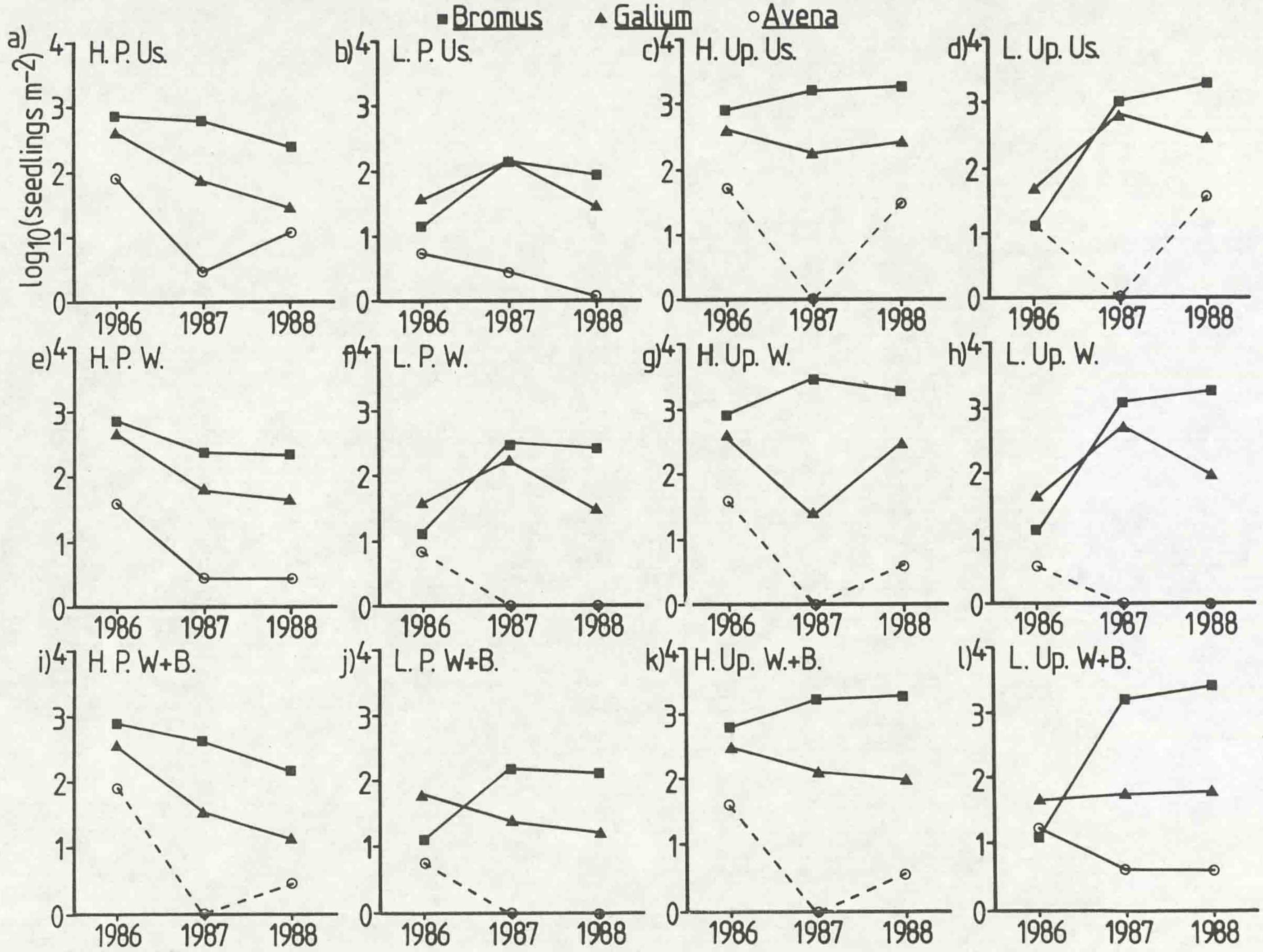


Figure 17. Trajectories based on seedling densities in March.
Treatments: Density: H High, L Low.
Cultivation: P Ploughed, Up Unploughed.
Herbicide: Us Unsprayed, W Wild oat herbicide, W+B Wild oat and broadleaf herbicides.

except *Avena* in Figure 16 b) changes in seed density are greater between 1985 and 1986 than between 1986 and 1987. This suggests that at least *Bromus* and *Galium* may be approaching an equilibrium. Approximate estimates of equilibrium values based on these data are 10000 *Bromus* seeds m^{-2}, 5000 *Galium* seeds m^{-2} and 400 *Avena* seeds m^{-2}. Under these two treatments, as well as almost all the others, yield of *Bromus* was slightly higher in 1986 than in 1987. This is unlikely to be due to the presence of a higher *Galium* density during the 1986-7 season since the effect was also seen in two treatments in which *Galium* density did not increase (Figures 16 i) and l)). It is more likely to be a result of an unknown climatic difference between the seasons which could affect *Bromus* on its own or its interactions with the crop or other weeds. The models of Chapter 5 predicted stable coexistence in a *Galium / Bromus* mixture. This appears to be the case in this 4 species weed mixture in which *Galium* and *Bromus* are the major components. However, the equilibrium seed density of *Galium* was very much lower than that predicted. This difference is probably not a consequence of seed loss on cultivation (not included in the models) alone since the *Galium* densities in the equivalent unploughed plots (Figure 16 c) and d)) were not significantly higher.

It was also predicted that in a mixture of *Bromus* and *Avena*, *Avena* would decline to extinction. In this 4 species weed mixture, however, the abundance (seed density) of *Avena* when not treated with herbicide appears to be moving towards approximately 400 seeds m^{-2}, from lower densities as well as from higher ones, and whether plots were ploughed or not. There are at least three possible explanations for this unexpected result.

The first is that the presence of *Galium* and *Sinapis* in the mixture affected the interaction between *Bromus* and *Avena*. Whilst the models of Chapter 5 suggested that the presence of *Galium* and *Sinapis* did little to affect the

yield of *Bromus* itself, it is not impossible that the interaction itself was altered.

The second possibility is that the assumption in the Hassell model that the equivalence coefficient α is constant across all densities and frequencies was violated.

The third possibility is that seasonal or site differences between the two experiments made the results of one inapplicable to the other. Site differences are unlikely to be a major source of error since the sites of the two experiments were adjacent fields of similar aspects and soil type. Seasonal differences may be investigated by comparing yields in the plots established in 1986 with those in ploughed, unsprayed plots established in 1985. This comparison is made in Table 12. The first and third rows of this table clearly show that *Bromus* yield was lower in 1986-7 than in 1985-6 (as suggested by the trajectories in Figure 16), whilst that of *Avena* was strikingly higher in 1986-7. Any effect on *Galium* is less clear and smaller, the ratios from high and low density plots lying either side of unity, and being closer to unity than those in the other species. The implication is that a "good" year for *Bromus* was a "bad" year for *Avena* and *vice versa*: this is a possible basis for non-equilibrium coexistence of these two species (Chapter 1). Comparison of ratios of 1987 yields in plots 1 and 2 years after sowing (rows 2 and 4, Table 12) with ratios of yields one year after sowing in plots sown in 1985 and 1986 (rows 1 and 3, Table 12) indicates whether the yields in the plots sown in different years were more similar the same length of time after sowing or within the same calendar year. For *Avena*, yields in the two sets of plots were far more similar in the same calendar year (1987) than in different calendar years the same length of time after sowing. This observation, coupled with the trajectories, suggests that seasonal effects may be more important than plot history in *Avena*, and populations may never reach equilibrium. The same effect was observed to a much lesser degree in

Table 12. Seasonal comparisons of yield. Yields of plots sown in 1986 and harvested in 1987 are compared with those of ploughed, unsprayed plots sown at low and high densities in 1985 and harvested in 1986 and 1987. Ratios are based on yields meaned across densities.

Density	Yield Ratio	Bromus	Avena	Galium
High	Ratio of yields after 1 year: sown 1986 / sown 1985	0.5	40	1.2
High	Ratio of yields in 1987: sown 1986 / sown 1985	1.7	0.9	3.1
Low	Ratio of yields after 1 year: sown 1986 / sown 1985	0.2	160	0.65
Low	Ratio of yields in 1987: sown 1986 / sown 1985	0.5	1.4	0.64

Table 13. Significance levels of F tests on the variance ratios from analyses of variance of harvest yield and seedling count data.

	Main and interaction sources	HARVEST 1986 B	G	A	HARVEST 1987 B	G	A	MARCH 1986 B	G	A	S	SEEDLING COUNTS 1987 B	G	A	S	SEEDLING COUNTS 1988 B	G	A	S
Main Plot	Block	NS	NS	NS	NS	NS	NS	*	***	NS	**	NS	NS	NS	NS	NS	NS	NS	NS
	Cultivation	NS	NS	NS	**	NS	NS	NS	NS	NS	NS	***	NS	NS	NS	***	***	*	NS
Sub Plot	Herbicide	NS	***	**	NS	***	***	NS	NS	NS	NS	NS	**	NS	*	NS	**	***	NS
	Density	NS	NS	**	NS	NS	***	***	***	***	**	***	**	NS	***	NS	NS	NS	***
	H x C	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	**
	C x D	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	H x D	NS	NS	NS	NS	NS	NS	NS	*	NS	NS	NS	***	NS	*	NS	NS	NS	NS
	H x C x D	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	*	NS	NS	NS	NS	NS	NS

Significance levels:

NS		p > 0.005
*	0.05 >	p > 0.01
**	0.01 >	p > 0.001
***	0.001 >	p

Species:

B: *Bromus*
G: *Galium*
A: *Avena*
S: *Sinapis*

Bromus. The trajectories based on seed density (Figure 16) suggest that equilibrium was more or less reached within a single season: hence, plot history was again not the dominant factor, but for a different reason. In *Galium*, however, yields from the two sets of plots were slightly more similar in different calendar years one year after sowing than in the same calendar year. This suggests that plot history was still more important than seasonal effects in *Galium*: this is compatible with the trajectories of seed density and the model prediction (Chapter 5) that *Galium* will reach an equilibrium level, but more slowly than *Bromus*.

Whilst this comparison of years suggests that *Avena* may avoid competitive exclusion by never reaching equilibrium due to seasonal fluctuations, it does not explain why the predictions of Chapter 5 were not fulfilled. The data on which the prediction that *Bromus* would drive *Avena* to extinction were based were yields in 1986-7, the "good" year for *Avena*. Hence, one of the other explanations, either the presence of *Galium* in the mixture or violation of the assumption of constancy of the parameter a, must be invoked to explain the failure of the predictions.

Considerable treatment effects on community trajectories can be seen in Figure 16. In contrast to the behaviour exhibited in unsprayed plots, *Avena* appeared to be declining towards extinction in those plots sprayed with wild oat herbicide (Figure 16 e) - l)). *Avena* seed yield in 1986 and 1987 was very low in these plots: most seeds present were thought to be dormant survivors of the initial seed input. In the plots treated with both the wild oat and broadleaf herbicides (Figure 16 i) - l)), *Galium* densities appeared still to be moving towards stable coexistence with *Bromus*, but at a lower equilibrium density. These results are consistent with the expected effects of the herbicides.

The main difference between ploughed and unploughed plots appears to be a *Bromus* seed density consistently higher by about 50% in the

unploughed plots. This is probably the result of a proportion of *Bromus* seeds being buried by ploughing to a depth from which they could not emerge.

Figure 17 shows community trajectories in terms of seedling densities in March, again based on mean values for each set of 3 replicates. Many of the effects seen clearly in seed density trajectories are less easily seen here. In the case of *Avena* this is probably due to the many zero values resulting from poor estimation of low densities. The difference in *Bromus* densities between ploughed and unploughed treatments was greater at the seedling stage, however. This is probably because the loss of seed by burial took place after the seed census but before the seedling count. Density dependent fecundity effects may have tended to reduce the effect on seed yield of the difference in plant density in March. On the other hand, the effect of broadleaf herbicide treatment on *Galium* was more clearly seen in seed than in seedling density; in this case the herbicide was applied after the seedling count was made.

This graphical treatment allows a comparison of the trajectories of the communities under a range of treatments and allows those treatments which have a pronounced effect on trajectories to be detected. In order to detect smaller or more transient treatment effects, data from each species at each census point were subjected to analysis of variance. Seed density data here are as harvested, and do not include an estimate of surviving, dormant seeds. Analyses of variance were carried out using the SAS package (SAS, 1985). Table 13 shows significance levels of F tests on the variance ratios for each main and interaction source of variation, based on Type III sums of squares. *Sinapis* has been omitted from the analyses of harvest data since no seeds were produced in any plot. Effects on seed density at harvest are clearest and in close agreement with those seen in the trajectories (Figure 16). There were no significant block effects, suggesting uniformity across the experimental site. Initial density had a significant effect only in *Avena*. This suggests that in *Bromus* and *Galium*, density dependent fecundity effects

had compensated for differences in initial plant density within a single season. *Avena* yields were still dependent on initial density in the 1987 harvest since most plants were likely to be derived from seed surviving from the initial sowing. Herbicide treatment also had a significant effect on *Avena* yields in both years. Examination of the data shows that this effect caused a depression of yield in plots sprayed with wild oat herbicide, as would be expected. Herbicide effects on *Galium* were significant in both years, the effect being a depression of yield when sprayed with wild oat and broadleaf herbicides. The only significant effect on *Bromus* was depression of 1987 yields in ploughed as opposed to unploughed plots, as seen in the trajectories. This effect was not seen in 1986 as the treatment was first applied after that harvest.

Examination of seedling densities in March census periods revealed significant treatment effects, which differed with time. Significant block effects were seen in 3 species in 1986, but not subsequently. This was probably because counts were made in each block in turn over a longer time period in 1986 than in the other years.

No cultivation or herbicide effects were seen in 1986 since treatments had not been applied by March. Significant cultivation effects were again seen in *Bromus* in 1987 and 1988, but in 1988 they were also seen in *Galium* and *Avena*.

The effect of ploughing was to reduce densities of *Galium* and *Avena*, but why this was not seen in 1987 is unclear.

Herbicide effects consistent with those observed on yields were seen in *Galium* in 1987 and 1988, and in *Avena* in 1988. A significant herbicide effect on *Sinapis* in 1987 was an unexpected result, since all 1987 seedlings are thought to have been derived from the seed sown in 1985. The large numbers of zero values scattered across all the treatments suggest that this is a spurious result arising from poor estimation of very low densities.

As would be expected, significant effects of initial density were seen in all species in March 1986, but as the communities moved from different initial compositions towards similar end points, only *Sinapis* showed a significant sowing density effect by March 1988. One anomalous result is the highly significant effect of initial density on *Bromus* seedling density in 1987. This is surprising since no such effect was observed in the 1986 harvest, and there is no evidence that *Bromus* seeds can survive dormant for a whole year. The most likely explanation is that effects of sowing density were present in 1986 *Bromus* yields, but were not detected due to experimental error associated with rather small harvest samples in that year and severe lodging in some plots. A few interaction terms were significant. Most of these were at low levels of significance, and could not be easily related to clear biological effects. The most significant was an effect of the interaction between herbicide treatment and density on *Galium* seedling density observed in March 1987. Inspection of the data suggests that this was related to a larger depression of *Galium* performance resulting from the 1986 application of broadleaf herbicide at low as opposed to high initial sowing densities. If this density dependent herbicide effect is real, it may not have been detected in the 1986 harvest because of experimental error associated with small harvest samples. It might not be expected to have been observed in March 1988 since there was a smaller difference in density between the two sowing treatments by the time the herbicide was applied in 1987.

Discussion.

It was argued in Chapter 5 that if difference equation models of interacting plant populations are to be of practical use in the management of weed communities, they must be tested over more than one year and beyond the range of the data used to formulate them. Further, they must be capable of extension in a simple fashion to incorporate the effects of different management practices. The results described in this chapter provide a partial test of the models of Chapter 5. The qualitative prediction of coexistence between *Bromus* and *Galium* in the presence of winter wheat is supported, even in the presence of two other weed species at low densities. As predicted, the mixture seems to move towards the same equilibrium from very different starting points. The quantitative prediction of equilibrium densities appears to have been grossly inaccurate. However, as shown in Chapter 5, varying parameter values suggested that little confidence should be placed in that prediction. The models of Chapter 5 suggested that in the presence of winter wheat, without herbicide, *Bromus* would drive *Avena* to extinction. It was concluded that some confidence could be placed in this prediction. Whilst *Avena* appears to be declining to extinction when treated with herbicide, these data do not support extinction of *Avena* when not sprayed. As discussed above, this discrepancy is likely to be due either to the influence of *Galium* which the models did not take into account, or failure of the Hassell model to fit the whole yield response surface accurately. The former possibility would not reduce the usefulness of this modelling approach in any way: the second would be a most serious criticism. There is no way of distinguishing between these two possibilities without further experimentation, and any such experiments would be of limited value since the performance of *Avena* has been shown to be highly susceptible to environmental fluctuation.

The results of this experiment also give some idea of the magnitude of the effects of different management practices, even though they are not sufficient to allow extension of the models to take them into account. In one case, the application of wild oat herbicide, a variation in management practice altered the community trajectory qualitatively, *Avena* declining towards extinction instead of apparently maintaining itself in the community.In two other cases the effects were only quantitative. Reduced cultivation led to an increase in estimated equilibrium *Bromus* seed density of the order of 50%. Application of broadleaf herbicide led to a very approximately 10-fold decrease in the estimated equilibrium seed density of *Galium*. The parameter variation exercises of Chapters 3-5 show that quite small changes in parameterization of Hassell models can be enough to cause changes of this magnitude in their predictions. The forms of the modified density responses would not necessarily be able to be fitted adequately by these models, however. An understanding of density or frequency dependence in plant responses to these practices would be needed in order to formulate models taking them into account. This understanding is entirely lacking.

This experiment provides strong evidence of coexistence between three weed species in the presence of winter wheat. A number of hypotheses explaining how species can avoid competitive exclusion and so coexist are given in Chapter 1. In some cases it is hypothesized that the coexisting populations are at equilibrium, in others they are taken never to achieve equilibrium. There is strong evidence that environmental fluctuations prevent *Avena* reaching equilibrium. Non-equilibrium coexistence with *Bromus* may be achieved as a result of "good" years for *Avena* being "bad" years for *Bromus* and *vice versa*. *Bromus* and *Galium*, however, appear to have been moving towards equilibrium coexistence. Possible explanations of equilibrium coexistence in the absence of herbivory include microsite differentiation, niche separation, and coexistence even when a limiting

resource is shared, due to relative competitive abilities varying with density and frequency in such a way as to allow coexistence at a certain density.

There is no information regarding microsite differentiation amongst species in these experimental plots apart from one tantalizingly small observation. During February 1986 there was a period of 2-3 weeks during which there were heavy white frosts each night with bright sunshine and strong, drying winds each day. Seedlings in the plots froze each night and were covered with ice in the mornings. They thawed rapidly as direct sunlight fell on them, allowing the time at which sunlight first fell directly on a plant to be measured easily. The parallel undulations in the ground resulting from ploughing, disc harrowing and drilling led to some small sites first receiving direct sunlight many minutes or even hours later than others. A linear regression of survivorship of autumn germinating *Sinapis* seedlings up to February in 0.2m x 0.2m sub-plots of each plot against minutes from dawn when the first *Sinapis* or *Galium* leaf or cotyledon in the same sub-plot received direct sunlight, showed a negative relationship with slope significantly different from zero (t test, $p<0.001$). Those microsites receiving direct sun earlier in the day were more favourable for the survival of *Sinapis*. This particular observation is of little direct significance, since all the autumn germinating *Sinapis* seedlings ultimately died, but it demonstrates that even in the apparently uniform environment of an arable field there can be biologically significant variation on a very fine scale. However, no obvious patterns of clustering with respect to microtopography were observed, and at least mature plants of *Galium* and *Bromus* are larger than the scale of variation discussed above.

It is more difficult to distinguish between the remaining possible explanations of equilibrium coexistence. The coexistence predicted by the models of Chapter 5 was due to density or frequency dependence in the outcomes of competitive interactions. However, the way in which the models

were fitted to experimental data means that any tendency to equilibrium present in the data, for whatever reason, would be interpreted in this way. *Bromus* and *Galium* are certainly very different morphologically and phenologically: niche separation is a strong possibility, but it cannot be demonstrated without further investigation.

It was stressed above that previous studies have demonstrated that the concept of stability in community structure must be related to the time scale of observation. Whilst it is concluded from observation and model that the communities are moving towards some fairly stable state, this stability is on the scale of a few years. Even in this artificially simple community protected from invasion by hand weeding, the effects of climatic change or soil impoverishment through continuous wheat cropping could well be great enough to alter any stable state which was transiently achieved.

Chapter 7.

General Discussion.

"The act of designing the model focuses the mind; it crystallizes the nature of problems in the real world of nature in the attempt to mimic parts of it in simple analogues."

Harper (1977)

In this chapter, two related questions will be addressed. The first is the question of how far the studies presented go towards the development of predictive weed population models: the second is that of how far they go towards interpreting the dynamics of simple plant communities.

Beginning at the level of interacting plant populations, the experiment described in Chapter 3 demonstrates that difference equation models may be fitted successfully to yield data from mixtures of three plant species in which all three species' densities are varied independently. Similarly, the experiment described in Chapter 5 demonstrates that such models may also be fitted to yield data from interacting weed populations in the presence of a crop, without explicitly taking the density or yield of the crop into account. Further, the models successfully incorporated persistent seed banks in two species. These three advances are all previously unreported extensions to this approach. Predictions of equilibria being reached in some populations

by convergent oscillations rather than monotonically (Chapters 3 and 5) also appears to be novel (but see Watkinson, 1981). It should be noted, however, that these are predictions rather than direct observations.

Three main grounds for inaccuracy of predictions based on models fitted to data from a single year are possible. The first arises when the predicted outcome of competition depends closely upon the precise parameter values of the fitted model. In such cases, even quite low levels of experimental error may lead to unacceptable imprecision in predictions. In the absence of a method for quantifying the error associated with the predictions made by a set of models of interacting populations, this source of inaccuracy was explored by examining the effect of varying each parameter estimate within its 95% confidence limits in a computer simulation. This had little effect on the qualitative predictions of the models of Chapters 3 and 5, allowing some confidence to be placed in them, but the predictions of the models of Chapter 4 were drastically altered, leading to rejection of those models as reliable predictors of community dynamics.

The second possible cause of inaccurate predictions is the fitting of an inappropriate form of model. The generally similar predictions of Hassell and Law and Watkinson models in Chapter 3 tends to justify the use of either form of model. The highly significant lack of fit of both Hassell and Law and Watkinson models for *Galium* populations (Chapter 5) suggests that an alternative form of model might have been appropriate, but apart from these points there is little evidence as to how important this source of inaccuracy may be.

The third possible cause of poor predictions is variation in environmental conditions between years. For the systems described in Chapters 3 and 4 there is no information so far on behaviour in more than one year, although this is currently being investigated. In the system described in Chapters 5 and 6 there is clear evidence of differences in performance of, in particular,

Avena between years (Chapter 6). The extent of the uncertainty that this would introduce into predictions of population and community dynamics is not clear. Whilst the models of Chapter 5 predicted that *Bromus* would drive *Avena* to extinction, the observations over $2^1/_2$ years in Chapter 6, albeit in the presence of two other weed species, tentatively suggest coexistence. Seasonal variation would not appear to be the only, or even the major cause of this inaccurate prediction, since the models were based on data collected during the 1986-7 season, in which *Avena* performed far better than in 1985-6. These possible sources of error in model predictions based on a single year's results highlight the importance of testing a model directly. This would entail the communities upon whose behaviour in one year the model was based to continue growing for one or more years, and comparing the observed community compositions with those predicted by the model. Whilst such tests are not described in this thesis, the models of Chapter 3 are being tested in this way during 1988, and will be reported elsewhere.

A number of points relating to the design of competition experiments have become apparent. The importance of a design which samples a range of both density and frequency has already been stressed, and need not be repeated. The range of densities chosen is crucial to the fitting of adequate models. Yield/density relationships when plotted on logarithmic axes generally show a region of maximum curvature associated with the transition from largely density independent individual yields at low densities to density dependent individual yields at higher densities. The experimental density range should ideally extend either side of this region of maximum curvature if the fitted model is to be used to make predictions at both low and high densities. The major problem encountered in the experiment described in Chapter 4 was that the density range was too high. Even in the experiment described in Chapter 3, the region of maximum curvature lay at the lower end of the density range. This was a result of using pots, which severely

limited minimum density whilst making it relatively easy to establish very high densities. In field systems, however, low densities can easily be established, whilst maximum density can be limited by the amount of seed available for large field plots. This tends to result in the region of maximum curvature being towards the upper end of the density range, as observed in the weed data of Chapter 5. From this argument, it might be expected that interactions at low density or low frequency, which may be important in the prediction of coexistence or competitive exclusion, may be poorly modelled from pot experiment data, whilst equilibrium densities may be estimated more accurately from pot experiments than field experiments. It is certainly true that some of the equilibrium weed densities predicted on the basis of field data in Chapter 5 were far from those observed in the long term experiment of Chapter 6. A compromise may be reached by carrying out experiments in the field but decreasing plot size as density increases. This, however, would introduce the problem of edge effects, already present in pot systems, to the field. Areas surrounded by a "guard" area can be sampled in larger plots, but this becomes impractical in small plots and pots.

Another important design point is raised by mixtures of species of determinate and indeterminate growth form. As discussed in Chapter 3, the later the harvest, the more a species with indeterminate form will be favoured in terms of relative yield. How should the time of harvest be determined? This is closely related to the problem of emergence time. A species emerging relatively early may be disproportionately successful in resource capture, and not all seeds sown together or even beginning to germinate at the same time emerge at once. A decision to sow all species at once is, then, biologically arbitrary, even if desirable on practical grounds. Decisions on the timing of sowing and harvest must depend on the aim of the experiment. If the aim of the experiment is to generate predictive models of practical value in a natural system, decisions on timing must be made so as to

emulate the natural situation. If, however, the aim is to understand better the basis of competitive interactions between the species, the timing of sowing and harvest should, ideally, be experimentally varied to investigate the effects of these factors. Mechanistic understanding and prediction may, then, be conflicting aims. The models described in this thesis are predictive, but in their inception most of the experiments were intended to give some mechanistic understanding as well as generating predictive models. Had either aim been pursued more closely, better predictive models or better mechanistic insights might have been achieved, but at the expense of scientific interest or practical application, respectively.

Two other design points arise, relevant specifically to weed systems in the field. The first is that of introducing the seed population at the beginning of the experiment. In these experiments, weed seeds were introduced after cultivation and sowing of the crop, and incorporated into the top 30mm of soil by raking. This is in contrast to the natural situation in which seed dispersal occurs prior to cultivation, which leads to a wider distribution of seeds through the soil profile. The most direct way of countering this problem would be to sow weed seeds immediately prior to cultivation, given that plots were large enough that transport between plots on tractor wheels or on the plough was not a serious problem, and given also that plots could reliably be located before and after cultivation. Neither seed transport nor plot location proved to be too serious a problem in the long term field experiment (Chapter 6). The second point is that this approach to the dynamics of interacting weed populations has been applied in these experiments only to serious weeds capable of severely reducing crop yield under some circumstances. By definition, these weeds must compete with the crop and competition between weed species is also then likely. A modelling approach based on density dependence might be expected to be more appropriate in mixtures of serious weed species than in species mixtures where

competition is less likely to be a major factor influencing yield. For example, some "fugitive" species appear to persist in arable fields, often at low density, by avoiding competition through growing mainly at the end of the crop's growing season, immediately before and after harvest. Examples in the U.K. include *Veronica* and *Kickxia* species. Investigation by this approach might not lead to accurate predictions of population and mixture dynamics of such species, but it might still allow testing of the hypothesis that it is competitive inferiority which forces the plants to adopt fugitive tactics.

Moving from the population to the community level, how far do these studies go towards understanding the dynamics of simple plant communities? The models developed in Chapters 2-5 allow community dynamics to be predicted, but in themselves give few clues to the mechanisms leading to competitive exclusion or coexistence of species, and equilibrium population sizes. Coexistence was predicted between *Bromus* and *Galium* in Chapter 5 and Chapter 6 describes results strongly suggesting coexistence between *Bromus*, *Galium* and *Avena*. A number of hypotheses to explain how competitive exclusion can be avoided are reviewed in Chapter 1. The most basic is the mathematical demonstration that equilibrium coexistence is possible in a truly uniform environment under certain conditions. It is this type of prediction which is made for *Bromus* and *Galium* in Chapter 5. The difficulty with this hypothesis is that in practice it is derived from a model fitted to experimental data. If the data suggest coexistence, for whatever reason, and the model fits well, then the model will predict equilibrium coexistence. The effects of any factor promoting coexistence will have been subsumed in the form of the model. This hypothesis, then, has almost no explanatory power. Other hypotheses depend upon whether coexistence is achieved when populations are at equilibrium levels or when equilibrium levels are prevented from being reached. It was argued in Chapter 6 that community trajectories tended to

show a movement towards equilibrium for, at least, *Bromus* and *Galium*. Coexistence predicted by this type of model must be either equilibrium coexistence or chaotic non-equilibrium coexistence. There was no evidence for or prediction of chaotic behaviour in any system. "Equilibrium" hypotheses to explain coexistence include niche diversification, non-uniformity of the habitat and differential predation or susceptibility to pathogens. Any of these explanations could underlie the form of the model. As discussed in Chapter 6, niche separation would appear to be the most likely explanation of coexistence in *Bromus* and *Galium*. Whilst many possible differences between the species present themselves, further experiments would be required to identify those differences which allow them to coexist. The only evidence supporting a "non-equilibrium" hypothesis comes from the coexistence of *Avena* and *Bromus*, which was not predicted by the models of Chapter 5. As suggested in Chapter 1, a "good" year for *Avena* (1986-7) appears to have been a "bad" year for *Bromus* (Table 12, Chapter 6). This is, however, only a tentative suggestion. A test would require the yields of a range of monocultures and mixtures of *Avena* and *Bromus* to be estimated in a number of different years.

The approach taken in this thesis has, in a small but definite way, succeeded in linking two levels of biological organization, the population and the community. At the level of the community it is reductionist and mechanistic, seeing communities in terms of their constituent, interacting populations. At the population level, the approach generates purely descriptive models, leaving the whole body of interacting causes at the individual level untouched. Population effects are seen as responses to density, whilst it is local resource availability which concerns the individual plant. Mechanistic understanding at the population, as opposed to the community, level is entirely lacking.

If the approach explored in this thesis has any practical value, it is likely to be in communities comprising relatively few, annual species, in a relatively simple, definable environment and with competition being a dominant factor leading to relatively clear density dependent effects. Whilst models could in theory be extended far beyond the level of Chapter 2 to include many more subtle and complex factors, it is experimental size and complexity which is likely to constrain the wider application of this approach. MacArthur (1972) in considering the approach in the wider context of species distributions of birds concluded "the greatest difficulty in testing the models of this section is only lack of ambition. It would be hard work to find the curves of the figures for different species [eg Figure 1 of this thesis] in different species, but it is not beyond present (1972) techniques." This thesis supports his view.

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Appendix 1

1000-seed weights of stocks used in experiments

Experiments described in Chapters 3 and 4

Triticum aestivum cv Bounty	43.0g
Avena sativa cv Dula	31.5g
Sinapis alba	6.1g

Experiments described in Chapters 5 and 6

Bromus sterilis	10.3g
Sinapis arvensis	2.26g
Avena fatua	21.3g
Galium aparine	11.1g

Appendix 2

Further notes on the selection of appropriate transormations of data when fitting models

The fitting of models to yield data, whether untransformed or transformed in various ways, makes certain assumptions about the error distribution in the data set. For example, if a model is fitted to untransformed data, it is assumed that yield is normally distributed about a mean value, with no dependence of variance of yield upon size of yield. If a model is fitted to log (yield) it is assumed that log (yield) is normally distributed and hence the variance of yield is proportional to mean yield.

Graphs of residuals plotted against fitted values were used to detect heterogeneity of variance and hence to decide which transformation most closely normalised the error structure inherent in each data set. For an optimal weighting or transformation of the data set, residuals need to be distributed homogeneously either side of the fitted values axis. These graphs were examined for each model fitted.

Appendix 3

Standard Errors of Seed Harvests and Seedling Counts

These data refer to the long-term field experiment (Chapter 6). Standard errors at each census point for each species are given, across treatments.

Seed harvests

Year	*Bromus*	*Avena*	*Galium*	*Sinapis*
1986	3520	0.352	820	-
1987	1320	27.3	433	-

Seedling counts

Year	*Bromus*	*Avena*	*Galium*	*Sinapis*
1986	15.8	4.39	8.84	9.73
1987	70.4	0.459	15.2	0.878
1988	95.0	1.64	10.3	2.53

Appendix 4

An example of parameter variation in simulation of the behaviour of fitted models

Simulations of the behaviour of fitted models involved iteration of the models, taking a wide range of starting values, for a large number of generations (30 to 100, depending on how quickly communities were predicted to move towards equilibrium). This process was repeated for each of a wide range of reparameterizations, as described in the text.

The following table summarizes this process, taking the Hassell models of *Bromus/Galium* mixtures (Chapter 5) as an example. Parameter values in the best fit model and in seven reparameterizations are given, with a summary of the behaviour of each model.

In each case, 5 initial compositions were used, 1:1, 100:100, 100000:100000, 1000;1 and 1:1000m^2.

Model	Species	K_3	K_4	b	α	S	Predicted Outcome
				Parameters			
	B	117	0.0265	0.713	-0.00628	0	Stable
Best fit	G	163	1.50	0.397	4.14	0.45	coexistence
Reparameterizations							
	B	117	0.0265	0.713	-0.00628	0	Stable
	G	163	1.50	0.397	4.14	0	coexistence
	B	117	0.0265	0.713	-0.00628	0	Stable
	G	163	1.50	0.397	4.14	0.5	coexistence
	B	151	0.0820	0.713	0.00628	0	Divergent
	G	904	22.0	0.397	4.14	0.45	oscillations under some starting conditions
	B	117	0.0265	1.04	-0.00628	0	Stable
	G	163	1.50	0.573	4.14	0.45	Coexistence
	B	117	0.0265	0.388	-0.00628	0	Apparently unlimited
	G	163	1.50	0.221	4.14	0.45	population growth
	B	117	0.0265	0.713	-0.0184	0	Behaviour varies with
	G	163	1.50	0.397	12.1	0.45	starting conditions
	B	117	0.0265	0.713	0.0184	0	Behaviour varies with
	G	163	1.50	0.397	-3.84	0.45	starting conditions

Appendix 5

Data from crop competition experiment (Chapter 3) meaned across replicates

Seeds m^{-2}					
SOWN			HARVESTED		
Wheat	Oats	Mustard	Wheat	Oats	Mustard
6.73	0	0	3210	0	0
21.5	0	0	7430	0	0
43.0	0	0	5690	0	0
129	0	0	11400	0	0
394	0	0	14500	0	0
1160	0	0	18100	0	0
3470	0	0	15400	0	0
10400	0	0	15700	0	0
25800	0	0	16000	0	0
64400	0	0	12300	0	0
172000	0	0	31700	0	0
0	8.00	0	0	12500	0
0	25.6	0	0	14700	0
0	51.2	0	0	17700	0
0	153	0	0	21300	0
0	322	0	0	32100	0
0	967	0	0	30100	0
0	2900	0	0	29400	0
0	8700	0	0	27700	0
0	21500	0	0	30200	0
0	53700	0	0	33100	0
0	14300	0	0	16800	0
0	0	7.46	0	0	58300
0	0	23.8	0	0	53600
0	0	47.8	0	0	85200
0	0	143	0	0	61100
0	0	322	0	0	66000
0	0	967	0	0	80500
0	0	2900	0	0	57700
0	0	8700	0	0	69200
0	0	21500	0	0	39200
0	0	53700	0	0	37800
0	0	143000	0	0	40200
21.5	25.6	0	5450	10800	0
43.0	102	0	3600	19700	0
64.4	76.8	0	7150	17600	0
85.9	51.2	0	7180	7020	0
129	307	0	5310	15500	0
193	230	0	8670	12900	0

Seeds m^{-2}					
SOWN			HARVESTED		
Wheat	Oats	Mustard	Wheat	Oats	Mustard
258	153	0	12400	10500	0
394	644	0	5110	21700	0
573	483	0	9310	15000	0
770	322	0	9980	12500	0
1160	1930	0	3750	20600	0
1740	1450	0	3630	19600	0
2330	967	0	4400	10500	0
3470	5800	0	2060	21800	0
5230	4350	0	919	17200	0
6960	2900	0	1650	13700	0
0	25.6	23.8	0	1670	37100
0	51.2	95.4	0	2470	42300
0	76.8	71.6	0	2130	46200
0	102	47.8	0	3800	38300
0	153	286	0	1840	51300
0	230	215	0	3770	57300
0	322	644	0	1550	49900
0	483	483	0	4680	46200
0	644	322	0	7820	44600
0	967	1930	0	2670	72900
0	1450	1450	0	5590	61300
0	2900	5800	0	1300	56400
0	4350	4350	0	2450	45400
0	5800	2900	0	5690	50600
21.5	0	23.8	1780	0	42200
43.0	0	95.4	800	0	50100
64.4	0	71.6	1250	0	51500
85.9	0	47.8	2950	0	25300
129	0	286	800	0	56900
193	0	215	3230	0	64900
258	0	143	4480	0	51100
394	0	644	1480	0	87600
573	0	483	2110	0	65600
770	0	322	5400	0	52300
1160	0	1930	746	0	54200
1740	0	1450	2800	0	52600
2330	0	967	4090	0	52700
3470	0	5800	257	0	65700
5230	0	4350	1870	0	48400
6960	0	2900	1960	0	50200
43.0	51.2	47.8	1530	1790	61300
21.5	25.6	95.4	817	716	77400
85.9	51.2	23.8	5070	2460	37500
21.5	102	23.8	758	3270	58000
129	153	143	2010	3380	61300

Seeds m^{-2}

SOWN			HARVESTED		
Wheat	Oats	Mustard	Wheat	Oats	Mustard
64.4	76.8	286	794	1280	62300
258	76.8	71.6	7670	3200	22100
64.4	311	71.6	1150	5810	59940
394	322	322	2700	3130	47600
193	230	644	740	1350	62600
770	230	215	5130	2440	28000
193	644	215	1570	6900	36600
1160	967	967	2040	4570	40500
573	483	1930	4180	1150	66200
2330	483	483	2120	4020	32000
573	1930	483	3820	9230	48600
3470	2900	2900	991	2970	46300
1740	1450	5800	513	1640	46600
6960	1450	1450	1850	2660	47500
1740	5800	1450	29.8	4610	35300

Appendix 6

Data from crop competition experiments in the presence and absence of herbicide (Chapter 4).Data shown are means across replicates

UNSPRAYED. WHEAT ; 0 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	-	0	0	0	0	0	0
	-	0	0	0	0	0	0
	-	53710	34520	61160	53770	50900	48700
5.91	0	-	-	-	-	-	-
	16930	-	-	-	-	-	-
	0	-	-	-	-	-	-
33.1	0	-	0	0	0	0	-
	36040	-	6590	1280	1164	71.6	-
	0	-	35330	52640	58660	58160	-
199	0	-	0	0	0	0	-
	29100	-	17760	10600	6283	716	-
	0	-	13840	23950	35640	24650	-
1289	0	-	0	0	0	0	-
	44110	-	41380	25190	9756	4529	-
	0	-	7661	39670	23610	36140	-
7733	0	-	0	0	0	0	-
	26690	-	36530	32920	24510	7944	-
	0	-	0	13680	9684	54420	-

UNSPRAYED. WHEAT: 22.01 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	5685	-	3643	1978	554.9	447.5	-
	0	-	-	-	-	-	-
	0	-	34290	36200	49440	32490	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	984.5	-	1718	1951	608.6	169.1	-
	17450	-	4940	1343	1683	948.7	-
	0	-	32650	62960	44300	79460	-
199	1122	-	0	295.4	-	322.2	-
	23080	-	18770	6623	-	1289	-
	0	-	24180	53090	-	68090	-
1289	465.4	-	0	474.5	5191	125.3	-
	34310	-	3367	20670	8844	7729	-
	0	-	8497	23110	21180	19120	-
7733	196.9	-	89.5	161.1	340.1	161.1	-
	31220	-	31500	26780	22410	11850	-
	0	-	125.3	3007	31950	38740	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

UNSPRAYED WHEAT: 132.6 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	8951	-	6140	3419	1826	1987	-
	0	0	0	0	0	0	-
	0	-	36000	16310	33630	44660	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	5430	-	7267	4296	1862	698.1	-
	11990	-	5102	608.6	89.5	143.2	-
	0	-	26660	60500	38340	56040	-
199	9747	-	3678	2792	1235	304.3	-
	15450	-	15000	5495	1020	3186	-
	0	-	20600	25020	46150	57580	-
1289	1862	-	1826	2596	805.5	537	-
	27690	-	19120	21960	12740	4529	-
	0	-	12100	14230	27230	43710	-
7722	233	-	1128	644.4	537	125.3	-
	27730	-	37450	32270	21500	13330	-
	0	-	465.4	20820	16920	36530	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

UNSPRAYED.WHEAT : 644.4 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	14310	-	10920	10290	4869	3115	-
	0	-	0	0	0	0	-
	0	-	2703	20780	47940	54230	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	10870	-	11460	9577	7518	3240	-
	2238	-	1862	2094	1074	0	-
	0	-	9290	29770	30300	47720	-
199	13840	-	11440	6158	5245	2775	-
	9360	-	7353	-	2864	71.6	-
	0	-	10010	16860	28660	49100	-
1289	8377	-	6909	3294	3571	2828	-
	24450	-	18080	-	5525	4117	-
	0	-	23480	26510	35550	32690	-
7733	2971	-	2954	2220	1002	1278	-
	25170	-	29320	24830	10470	10200	-
	0	-	5334	10260	45650	41400	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

UNSPRAYED.WHEAT : 3866 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	14480	-	13480	14480	-	6587	-
	0	-	0	0	-	0	-
	0	-	-	19670	-	33380	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	18830	-	14410	17940	13280	6891	-
	3902	-	859.2	53.7	53.7	17.9	-
	0	-	2041	15190	21480	34490	-
199	14160	-	14250	12940	12080	7715	-
	4207	-	2488	626.5	1307	483.3	-
	0	-	1432	15990	23750	43910	-
1289	10550	-	10130	9845	8198	6140	-
	8482	-	11760	6856	5782	2041	-
	0	-	1074	10890	19240	38700	-
7733	7339	-	9254	6892	6247	2434	-
	21270	-	25290	18670	14560	7464	-
	0	-	554.9	9165	23400	32900	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

SPRAYED. WHEAT ; 0 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	-	0	0	0	0	0	0
	-	0	0	0	0	0	0
	-	29840	38470	48130	39800	34900	49350
5.91	0	-	-	-	-	-	-
	24350	-	-	-	-	-	-
	0	-	-	-	-	-	-
33.1	0	-	0	0	0	0	-
	24960	-	12350	7844	2309	17.9	-
	0	-	20300	21160	5048	42650	-
199	0	-	0	0	0	0	-
	34680	-	26310	6068	4296	2291	-
	0	-	17290	50160	26330	44440	-
1289	0	-	0	0	0	0	-
	46500	-	38500	19510	10490	689.2	-
	0	-	6050	5030	38470	18600	-
7733	0	-	0	0	0	0	-
	35940	-	35620	27690	29820	15420	-
	0	-	895	5424	14540	19390	-
46400	0	-	-	-	-	-	-
	36840	-	-	-	-	-	-
	0	-	-	-	-	-	-

SPRAYED.WHEAT : 22.01 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	3763	-	3974	17360	1002	214.8	-
	0	-	0	0	0	0	-
	0	-	0	34670	40830	47360	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	2461	-	2703	1038	411.7	0	-
	5834	-	11230	3374	3634	1539	-
	0	-	20210	37630	24110	37750	-
199	2399	-	1092	1620	250.6	465.4	-
	10970	-	25850	11020	4493	591.1	-
	0	-	5222	19830	25600	34710	-
1289	447.5	-	1038	134.3	554.9	0	-
	41130	-	27660	30690	12690	2399	-
	0	-	0	12570	22840	52810	-
7733	232.7	-	107.4	125.3	125.3	71.6	-
	35210	-	30520	41380	20100	15180	-
	0	-	-	3580	8843	26580	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

SPRAYED WHEAT: 132.6 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	9462	-	8100	2840	2882	698	-
	0	-	0	0	0	0	-
	0	-	7232	32400	43480	63370	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	7446	-	7616	5307	2327	1253	-
	10370	-	8113	1709	698.1	107.4	-
	0	-	11180	28550	42170	61090	-
199	7518	-	6712	2640	2041	429.6	-
	27350	-	14100	9520	3652	125.3	-
	0	-	1298	14370	15450	34440	-
1289	4654	-	2882	2184	698.1	214.8	-
	28550	-	33690	20620	10810	3902	-
	0	-	0	16770	12580	32580	-
7733	823.4	-	966.6	358	1325	411.7	-
	31160	-	38270	39420	19890	14230	-
	0	-	0	0	79935	9738	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

SPRAYED.WHEAT : 644.4 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	14095	-	13340	11260	7715	2631	-
	0	-	0	0	0	0	-
	0	-	6372	22410	25510	45430	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	13400	-	14050	10670	5818	3150	-
	4923	-	3491	4189	322.2	304.3	-
	0	-	2900	15160	6211	33470	-
199	10880	-	15110	10380	5155	2954	-
	10590	-	2882	5352	2721	2631	-
	0	-	19600	6247	10000	31520	-
1289	7303	-	7500	5943	4207	1665	-
	20620	-	17790	14680	9108	2470	-
	0	-	0	3849	14840	33100	-
7733	787.6	-	1808	2792	1951	1396	-
	24180	-	32810	25790	17490	13620	-
	0	-	0	8395	6874	18720	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

SPRAYED-WHEAT : 23200 plants m^{-2}

OATS (plants m^{-2})	MUSTARD (plants m^{-2})						
	0	3.76	20.4	124	716	4300	25800
0	15995	-	18150	15500	15570	8628	-
	0	-	0	0	0	0	-
	0	-	9254	2238	18470	27640	-
5.91	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
33.1	1030	-	15170	11560	10310	9254	-
	1486	-	1164	501.2	644.4	358	-
	0	-	-	1790	12550	14570	-
199	12927	-	14070	15970	10740	9004	-
	2094	-	8878	2076	841.3	1146	-
	0	-	1897	14250	14230	21500	-
1289	12125	-	11900	11440	9648	7800	-
	7371	-	7339	5048	7214	2417	-
	0	-	0	1665	3347	24990	-
7733	8699	-	5334	6176	7142	3464	-
	22570	-	23150	23340	14620	1100	-
	0	-	0	4457	20890	16770	-
46400	-	-	-	-	-	-	-
	-	-	-	-	-	-	-
	-	-	-	-	-	-	-

Other treatments not included in tables

	Sown (seeds m^{-2})			Harvested (seeds m^{-2})		
	Wheat	Oat	Mustard	Wheat	Oats	Mustard
Sprayed	23200	0	0	16000	0	0
	3.94	0	0	4661	0	0
Unsprayed	23200	0	0	14350	0	0
	3.94	0	0	3854	0	0

Appendix 7

Data from weed competition experiments (Chapter 5).

Data shown are means across replicates

Single Weed species

Bromus

Seeds sown m^{-2}	Seeds harvested m^{-2}
0.845	141.5
3	363.6
20	1545
140	3839
1000	20026
2000	14672

Galium

Seeds sown m^{-2}	Seeds harvested m^{-2}
0.920	128.0
4	473.7
27	1030
186	4763
1330	12327
2670	13363

Avena

Seeds sown m^{-2}	Seeds harvested m^{-2}
2.11	38.07
50	289.6
333	647.5
2330	1496
16700	1756

Sinapsis

Seeds sown m^{-2}	Seeds harvested m^{-2}
3.15	0
15	0
100	0.445
700	52.61
5000	252.5

Bromus/Galium mixtures

Each cell in the table shows : *Bromus* seed harvested m^{-2}

Galium seed harvested m^{-2}

Bromus seed sown m^{-2}	*Galium* seed sown m^{-2}				
	0.920	4	27	186	1330
0.845	75.6 37.0	114 456	104 510	130 5920	73.8 8920
3	1190 56.9	370 182	356 781	107 4990	338 15800
20	614 41.6	3760 164	1240 520	3180 4410	7830 8270
140	8700 69.1	1960 0	8770 883	3180 860	1940 6570
1000	11700 252	13000 16	13000 408	154000 472	6030 2040

Bromus/Avena mixtures

Each cell in the table shows : *Bromus* seed harvested m^{-2}

Avena seed harvested m^{-2}

Bromus seed sown m^{-2}	*Avena* seed sown m^{-2}				
	2.11	50	333	2330	16700
0.845	109 42.7	107 225	58.9 414	119 996	37.8 1900
3	218 25.3	599 153	127 2580	480 988	718 1710
20	2600 28.7	1350 123	3170 1800	1210 2070	883 1730
140	4460 67.6	4720 120	8090 260	3570 675	5160 3030
1000	6250 0	6270 44.5	10600 156	7810 192	12100 1670

Bromus/Sinapis mixtures

Each cell in the table shows : *Bromus* seed harvested m^{-2}

Sinapis seed harvested m^{-2}

Bromus seed sown m^{-2}	*Sinapis* seed sown m^{-2}				
	3.15	15	100	700	5000
0.845	184 0	120 0	224 18	181 19	94.4 201
3	341 4	292 0	348 1.48	538 48	343 360
20	2380 0	1730 0	1560 0	2130 24	940 334
140	6440 0	4480 0	6060 0	6360 -	6730 -
1000	18300 0	6370 0	- -	5510 -	7770 -